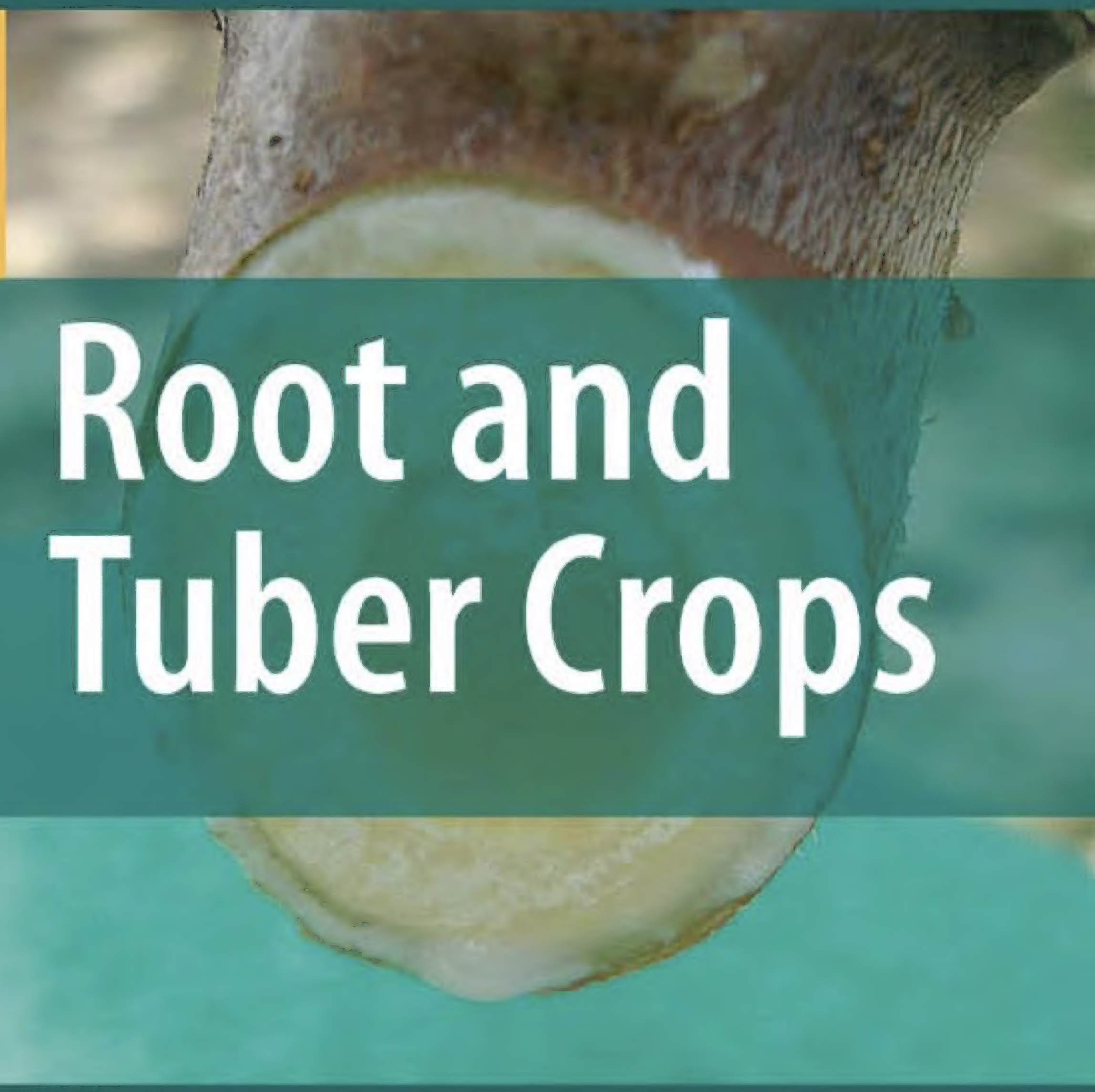
HANDBOOK OF PLANT BREEDING

J.E. Bradshaw
Editor



Root and Tuber Crops

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HANDBOOK OF PLANT BREEDING

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Preface

This volume in the *Handbook of Plant Breeding* covers ten root and tuber crops in eight chapters: potato (*Solanum tuberosum*), cassava (*Manihot esculenta*), sweet potato (*Ipomoea batatas*), yams (*Dioscorea* spp.), taro (*Colocasia esculenta*) and cocoyam (*Xanthosoma sagittifolium*), sugar beet (*Beta vulgaris*), fodder beet (*Beta vulgaris*), and swedes (*Brassica napus*) and turnip (*Brassica rapa*). Although many of these crops were first domesticated several thousand years ago, none became important on a global scale until after the end of the sixteenth century. This brief introduction is a broad overview and inevitably a simplification of the details which follow in the individual chapters where unresolved issues are discussed.

The potato was domesticated in South America, cassava probably in South America but possibly in Mexico, and sweet potato probably in Mexico but possibly in South America, some 8,000 years ago. All three crops have wild relatives in both Central and South America. Much later, after Columbus discovered the New World in 1492, European sailors introduced the potato to Europe and from there to many other parts of the world, and both cassava and sweet potato to Africa and then Asia. Interestingly, the sweet potato was being grown in Oceania before Columbus, but the routes of introduction are still debated. Today the potato is the third most important food crop in the world, after wheat and rice, and the four largest potato producing countries are China, the Russian Federation, India, and the USA. Cassava is the most important root and tuber crop in the tropics where it is a primary staple food in many of the poorest countries, with the largest production in Nigeria, Brazil, Thailand, and Indonesia. The sweet potato is also a food staple in Asia, Africa, and America, but with production dominated by China, where half of the crop goes for animal feed. Yams are also important staple food crops in tropical and subtropical regions. The four main cultivated yams were independently domesticated on three continents some 7,000 years ago: *Dioscorea rotundata* and *D. cayenensis* in West Africa, *D. alata* in Southeast Asia and the South Pacific, and *D. trifida* in South America. Today, however, the major producers are in West Africa: Nigeria, Ivory Coast, Ghana, and Benin. Although taro and cocoyam are minor crops, they do provide a staple food for poor people in Africa, Asia, and America. Taro was domesticated some 10,000 years ago in Asia, Southeast Asia, and Melanesia, whereas cocoyam was domesticated in South America and subsequently taken in the sixteenth century to Africa and then Asia. Today the main producers of these crops are

Nigeria, Ghana, and China. The relative importance of all these crops can be seen from the 2008 FAO production statistics (http://faostat.fao.org): potato (314 million tonnes), cassava (233), sweet potato (110), yams (52), and taro and cocoyam (12); with sugar beet at 228 million tonnes.

The edible storage organs are underground tubers for potatoes and yams, storage roots for cassava and sweet potato, and corms/cormels for taro and cocoyam. All of these organs store energy as starch and the crops are viewed primarily as sources of carbohydrate energy when used as a food staple. They are, however, also valuable sources of minerals, vitamins, and other antioxidants. In addition, there is a trend toward using them to produce processed products for both human consumption and industrial use. All of the crops are vegetatively propagated: potatoes and yams through their tubers, cassava as stem cuttings, sweet potato as vine cuttings, and taro and cocoyam through side shoots, stolons, or corm heads. These propagation methods are slow, so more rapid ones have been, and are being, developed for the breeding and multiplication of new cultivars.

In contrast, sugar beet, fodder beet, swedes, and turnips are grown from true botanic seed and their above-ground storage organs are swollen hypocotyls with varying amounts of stem above and root below, often simply referred to as 'roots.' Their carbohydrate is primarily in the form of simple sugars, sucrose in beets and glucose and fructose in swedes and turnips. Sugar beet and fodder beet were both derived from the leaf and table beets grown as vegetables by the Greeks and Romans. Fodder beets, with larger roots, were developed during the 'Middle Ages' in Northern Europe for livestock fodder and became an important winter feed for cattle from the 1800s. After the discovery that temperate fodder beets contained the same kind of sugar as tropical sugarcane, the first sugar factory opened in Silesia (Poland) in 1802, and sugar beets were selectively bred from the 1800s. Today sugar beet provides about one-quarter of the world's sugar production from crops grown in temperate climates such as found in Europe and the northern USA.

The turnip, like table beet, was also a vegetable grown by the Romans, and probably the Greeks before. The turnip came to prominence as an agricultural crop as part of the four-field rotation (wheat, turnips, barley, and clover) which originated in Flanders and was introduced into Britain by Lord 'Turnip' Townshend about 1730. This led to the British Agricultural Revolution of the eighteenth and nineteenth centuries, which enabled the population base for the Industrial Revolution to take place. The origin of *B. napus* (swedes, oilseed, and forage rape), the allotetraploid of *B. rapa* (turnips) and *B. oleracea* (kales and cabbages), is uncertain, but it appears to have arisen several times in recent history. Swedes were first recorded in Europe in 1620 and introduced to Britain around 1780, where they were favored over turnips as having better keeping and feeding quality. By around 1870 the area of swedes and turnips in Britain had peaked at almost 1 million hectares. Today fodder beet, swedes, and turnips are minor crops for feeding to livestock in temperate climates such as Northern Europe and New Zealand, with swedes and turnips also grown as vegetables for culinary use. They have been replaced as major crops for animal feed by cereals and silage.

Since domestication, all of the crops have been improved by both conscious and unconscious farmer selection. More modern hybridization and selection by farmers, hobby breeders, and seedsmen occurred for potato, sugar beet, fodder beet, swedes, and turnips during the nineteenth century. These crops were therefore well placed to benefit from the birth of modern genetics in 1900 and the subsequent development of scientific breeding methods. Thus, for example, methods of producing hybrid cultivars to exploit heterosis for yield are available in the four crops grown from true botanic seed. Modern breeding of cassava and sweet potato started in the 1920s, but intensified really only from the 1960s and 1970s when breeding work also started to get underway for yams, taro, and cocoyams. This modern breeding work has been helped by the establishment of International Research Centers aimed at providing food security and eradicating poverty in developing countries; and this will remain important during a period of human population growth and climate change.

The extent to which the crops are benefiting from new biotechnologies reflects both their own economic importance and that of their close relatives. Thus the potato and cassava genomes have already been sequenced and that of sugar beet is due in 2011. Fodder beet breeding will benefit from advances with sugar beet and swedes and turnips from advances in their oilseed relatives. Molecular markers are available in all of the crops and are being used to characterize germplasm as well as resolve issues over domestication. Molecular marker maps have been produced and there are varying degrees of progress in using them for marker-assisted selection. Likewise genetic transformation is either available or becoming available to complement conventional breeding. It should be of particular value in the vegetatively propagated polyploids with complex inheritance patterns such as potato and sweet potato.

The new biotechnologies need to build on and integrate with past progress in breeding. It is still important to appreciate the reproductive biology of the crop, its evolutionary history, and the germplasm available to breeders. All of this is covered in each chapter in this volume, together with breeding methods and objectives, which fall into the broad categories of higher yields, better quality, and improved disease and pest resistance. While all of the harvested products of the crops considered are vegetatively produced storage organs, their breeding involves sexual hybridization and hence a knowledge of flowering, pollination, and seed set. In this respect, sugar and fodder beet, and swedes and turnips, are biennial species with a vernalization requirement for flowering. Swedes, unlike the other crops, are self-fertile and tolerant of inbreeding, despite being insect pollinated and having progenitors with sporophytic self-incompatibity. As expected, natural self-pollination occurs in potatoes as gametophytic self-incompatibility breaks down in polyploids, but the crop is not tolerant of inbreeding. Natural pollination is normally by wind in sugar and fodder beet and by insects in the other crops. Out-crossing is encouraged in some species by separate male and female plants (yams) or flowers (cassava, taro, and cocoyam), as well as by protogyny. In other species self-pollination is prevented by self-incompatibility which is gametophytic in sugar and fodder beet and sporophytic in sweet potato and turnip. Some of the crop species are regarded as diploids (cassava, taro, cocoyam, sugar and fodder

beet, and turnip), although sugar and fodder beet cultivars can be triploid as well as diploid hybrids, whereas other species are clearly polyploids. Swedes are an allotetraploid and the principal cultivated potato is an autotetraploid. Sweet potatoes are hexaploid (probably an allo-autopolyploid as a result of being a hybrid between a diploid and tetraploid species), and yams form a polyploid series, and incidentally are monocotyledonous.

Finally, there are also nine lesser known root and tuber crops native to the Andes of South America and cultivated by indigenous farmers. They have edible underground organs and are used both as subsistence and cash crops. Not enough breeding work has been done on them to justify a chapter in this volume, but further information is available from the International Potato Center (CIP) in Lima, Peru (http://www.cipotato.org), where accessions have been 'Held in Trust' since 1990 in their genebank, and some research has been done. A few brief comments will indicate why they are of interest. Achira (*Canna indica*) has rhizomes which contain large starch granules and hence high-value starch. It is also grown in Vietnam for noodles. Ahipa (*Pachyrhizus ahipa*) is a legume crop which produces carbohydrate-rich (starch and sugars) tuberous roots. Arracacha (*Arracacia xanthorrhiza*) has tuberous storage roots which provide starchy food free from undesirable substances. It has been introduced to Brazil where some breeding work is being done. Maca (*Lepidium meyenii*) is a root crop that can be grown at the upper altitude limits for agriculture and is of interest for its medicinal properties. Mashua (*Tropaeolum tuberosum*) produces yellow-fleshed tubers with a high carbohydrate content, both starch and sugars. Mauka (*Mirabilis expansa*) has fleshy edible storage roots high in carbohydrate and protein. Oca (*Oxalis tuberosa*) is a tuber crop which has also been grown in New Zealand for over a century, and where recent breeding work has led to the release of a new cultivar. Ulluco (*Ullucus tuberosus*) produces starchy tubers and has also been introduced to New Zealand as a new food crop where some research has been done on its yellow and red betalain pigments. Yacon (*Smallanthus sonchifolius*) produces non-starchy roots which contain high levels of sugars and fructooligosaccharides which can be used as sweeteners for diabetics. It was introduced from New Zealand to Japan in 1985 where a new cultivar, Saradaotome, has been bred.

In order to provide uniformity with the other volumes in the *Handbook of Plant Breeding*, each chapter is divided into the following sections: Introduction, Origins and Domestication, Varietal Groups (where appropriate), Genetic Resources, Major Breeding Achievements, Current Goals of Breeding, Breeding Methods and Techniques, Integration of New Biotechnologies in Breeding Programs and Seed (Tuber/Commercial) Production. The length of each section varies with crop, as appropriate, and I tried to give the authors of chapters as much freedom as possible within this overall framework. We hope that the finished product will be of value both to students of plant breeding and professional plant breeders, as well as to anyone interested in this fascinating group of root and tuber crops.

I would like to thank Jaime Prohens for asking me to edit a volume in the *Handbook of Plant Breeding*, the authors of chapters for their contributions and co-operation, and Hannah Schorr of Springer for all of her help and encouragement, it was much appreciated.

Dundee, Scotland John E. Bradshaw

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Chapter 1
Potatoes

John E. Bradshaw and Merideth Bonierbale

1 Introduction

The potato (*Solanum tuberosum*) is the world's third most important food crop after wheat and rice with 309 million tonnes fresh weight of tubers produced in 2007 from 18.5 million hectares of land (http://faostat.fao.org). Half of the potato production in 2007 (150 million tonnes) was in Asia, Africa, and Latin America as a result of steady increases in recent years, particularly in China and India. Indeed, China (56 million tonnes, down from 71 in 2005) is now the number one potato producer in the world and India (22 million tonnes) is third, with the Russian Federation (37 million tonnes) second, and the USA (20 million tonnes) fourth. In contrast, the order for kg/capita/year consumption in 2003 was Russia (125), USA (63), China (35), then India (17) (http://faostat.fao.org), and the provisional figures for 2005 were similar. However, actual rates and impact are highly variable within countries once disaggregated data are reviewed. The increases in production in China have primarily been through increases in the area of potatoes planted (4-fold since 1960), but accompanied by some increases in yield/hectare (1.5-fold since 1960), whereas in India there have been equal contributions (3-fold and 2.5-fold, respectively). As a major food staple the potato is contributing to the United Nation's Millennium Development Goals of providing food security and eradicating poverty, which is helped where the potato provides not only food but also employment and income as a cash crop. In recognition of these important roles, the UN named 2008 as the International Year of the Potato.

More information on potatoes can be found in the following books: *Genetic Improvement of Solanaceous Crops Volume I: Potato* (Razdan and Mattoo, 2005); *Handbook of Potato Production, Improvement, and Postharvest Management* (Gopal and Khurana, 2006); *Potato Biology and Biotechnology, Advances and*

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Perspectives (Vreugdenhil, 2007); *Propitious Esculent, The Potato in World History* (Reader, 2008); and *Advances in Potato Chemistry and Technology* (Singh and Kaur, 2009).

1.1 Nutritional Value

The potato tuber is a subterranean swollen stem which evolved to survive from season to season as a dormant storage organ. The form of energy storage is almost entirely starch. Potatoes are thus a major source of carbohydrate energy in the diets of hundreds of millions of people and are even being considered for human life support in space (Wheeler, 2009). A small but significant portion of potato starch is resistant to digestion by enzymes in the stomach and small intestine and so reaches the large intestine essentially intact. This resistant starch is considered to have similar physiological effects and health benefits as fiber: it provides bulk, offers protection against colon cancer, improves glucose tolerance and insulin sensitivity, lowers plasma cholesterol and triglyceride concentrations, increases satiety, and possibly even reduces fat storage. The amount of resistant starch in potatoes depends much on preparation methods. Cooking and then cooling potatoes have been reported to significantly increase resistant starch. For example, Englyst et al. (1992) showed that about 7% of cooked potato starch is resistant starch, but that this percentage increases to about 13% upon cooling.

While potatoes are commonly perceived as a carbohydrate source, they are also a good source of high-quality protein. Although potatoes contain only about 2% protein on a fresh-weight basis, the value increases to about 10% when examined on a dry-weight basis, equal to that of most cereals such as rice or wheat. Potatoes provide an excellent source of lysine, but low contents of sulfur amino acids limit their nutritive value (Friedman, 1996). They also provide significant amounts of vitamins C, B6 and B1, folate, the minerals potassium, phosphorus, calcium, and magnesium, and the micronutrients iron and zinc. Potassium is the most abundant of the minerals. The concentration of iron and zinc in potato is low compared with the concentration of these micronutrients in cereals and legumes. However, the bioavailability of iron in potato is greater than in cereals and legumes due to the presence of high levels of ascorbic acid (promoter of iron absorption) and low levels of phytic acid (inhibitor of iron absorption) (Fairweather-Tait, 1983).

Potatoes are high in dietary fiber, especially when eaten unpeeled with their skins, and are rich in antioxidants comprising polyphenols, vitamin C, carotenoids, and tocopherols (Storey, 2007). Cooking reduces the concentration of vitamin C in tubers. However, the degree of the reduction depends on the cultivar and on the way of cooking. A recent study using native potatoes from the Peruvian Andes found that the concentration of vitamin C in tubers boiled with their skin was higher than those that had been baked or cooked in a microwave oven (Burgos et al., 2009a). One hundred grams of cooked potatoes can contribute 25–50% of the daily recommendation of ascorbic acid (100–120 mg/day) (Naidu, 2003).

The concentration of carotenoids in potato tubers is related to flesh color. Yellow-fleshed potatoes have high concentrations of total carotenoids, varying up to 1,840 μg/100 g on a fresh-weight basis with zeaxanthin being the principal one (Burgos et al., 2009b). Cream-fleshed potatoes have low concentrations of total carotenoids, with lutein, vioaxanthin, and beta-carotene being the principal ones. Lutein and zeaxanthin, two of the carotenoids of higher concentration in human serum, are localized in significant quantities in the retina and play a part in protecting against macular degeneration. The concentration of zeaxanthin in yellow-fleshed potato tubers reaches 1,290 μg/100 g on a fresh-weight basis. This particular characteristic of yellow-fleshed potatoes is of great importance because dietary sources of zeaxanthin are scarce. It seems that cooking has no negative effect on the lutein and zeaxanthin concentrations of potatoes. One hundred grams of the cooked yellow-fleshed varieties provide a significant amount of zeaxanthin (above 500 μg) to the human diet (Burgos et al., 2009b).

All potatoes contain chlorogenic acid as the principal phenolic acid. Red and purple potatoes also contain anthocyanins. Whole unpeeled potatoes with fully pigmented flesh can have up to 40 mg/100 g FW total anthocyanins. Red-fleshed potatoes contain acylated glucosides of pelargonidin, while purple potatoes contain in addition, acylated glucosides of malvidin, petunidin, peonidin, and delphinin (Brown, 2005). Due to their anti-oxidative properties, phenolic compounds have potential health benefits, possessing antibacterial, antiviral, anticarcinogenic and anti-inflammatory properties, and vasodilatory action (Mattila and Hellstrom, 2006). Potato tubers with red and purple flesh are a rich source of phenolic compounds in the diet (Al-Saikhan et al., 1995). Cooked tubers have shown higher concentrations of phenolic compounds that may be attributable to more efficient extraction from cooked samples (Burgos et al., 2009c).

As a staple food and as a vegetable, potatoes need to be cooked because of the indigestibility of their ungelatinized starch (Burton, 1989). Such cooking is frequently by baking, boiling, steaming, roasting, deep-oil frying, or microwave cooking, although in their native Andes a broad diversity of additional preparation methods are employed. When baked, boiled or mashed and eaten alone, potatoes generally have a high glycemic index (GI) which is a measure of the effect of the consumption of a carbohydrate food on blood glucose levels. Thus the high GI of potatoes became of concern for type 2 diabetics, and more generally for the rising levels of obesity in many countries (Foster-Powell et al., 2002), whereas it was considered beneficial to sports persons after exercise because it produces a rapid supply of muscular glycogen. However, Monro and Mishra (2009) have pointed out that GI is short for GI of available carbohydrate and this is much higher than the relative glycemic impact or potency of potato per se. Indeed, boiled and mashed potatoes are not highly glycemic, being similar to boiled spaghetti and rice on an equal fresh weight basis. Furthermore, potatoes are usually eaten in mixed meals and their nutritional value means that they are generally a very useful and beneficial component of the human diet (McGregor, 2007). Monro and Mishra (2009) concluded from their review that potatoes have an important role as a benign source of moderate-density carbohydrate energy that fits comfortably into a range of

balanced diets. Fresh potatoes are virtually free of fat and cholesterol and have a water content of about 80%.

1.2 Processed Products

The commercial value of potatoes is increased considerably when they are processed into edible products that appeal to consumers on flavor, texture, appearance, and most of all convenience (Kirkman, 2007). Today the major processed products are potato crisps (chips), French fries, and other frozen products, followed by dehydrated products, chilled-peeled potatoes and canned potatoes. Industrial production of crisps (chips) started in the 1920s and French fries in the 1950s, and potato processing has since grown into a global industry which is still expanding. In North America and some European countries between 50 and 60% of the crop is processed (Li et al., 2006; Kirkman, 2007). Furthermore, processors are building factories in countries where the potato is primarily grown as a staple food, and this is a trend that is likely to continue. Kirkman (2007) has estimated that global consumption in processed form will have increased from 13% of total food use in 2002 to nearly 18% by 2020.

Since the first potato starch plant was established in the USA in the 1830s (Treadway, 1959), the industry has developed in North America and Europe, particularly in the Netherlands, Poland, France, and Germany (Burton, 1989). Today potato starch is the starting material for the preparation of more than 500 different commercial products (Davies, 2002). Since the 1990s, potatoes have proved useful for molecular farming whereby plant cells are used to express recombinant genes and produce value-added products such as vaccines (Li et al., 2006). In some countries potatoes are still fed to animals but this use is decreasing.

1.3 Production

Potatoes are grown in 149 countries from latitudes 65°N to 50°S and at altitudes from sea level to 4,000 m (Hijmans, 2001). Potatoes can be grown wherever it is neither too hot (ideally average daily temperature below 21°C) nor too cold (above 5°C), and there is adequate water from rain or irrigation (Govindakrishan and Haverkort, 2006). In practice this means that they are grown as a summer crop in the tropical highlands of Bolivia, Peru, and Mexico; all the year round in parts of China and Brazil and in the equatorial highlands of South America (e.g., Ecuador and Colombia) and East Africa (e.g., Kenya and Uganda); as a winter crop in the lowland subtropics (e.g., northern India and southern China); as spring and autumn crops in the Mediterranean (e.g., North Africa); and in summer in the lowland temperate regions of the world (North America, western and eastern Europe, northern China, and Australia and New Zealand).

The growing season can be as short as 75 days in the lowland subtropics, where 90–120 days is the norm, and as long as 180 days in the high Andes. In the lowland temperate regions where planting is done in spring and harvesting in autumn, crop duration is typically 120–150 days and yields are potentially high. Modern potatoes have a high harvest index of around 0.80 (the proportion of the whole plant's dry weight which is harvestable tuber) and experimentally, tuber fresh-weight yields of 120 tonnes/ha have been achieved in Western Australia with a long growing season in the absence of pests and pathogens and with adequate inputs of water and fertilizers (Mackay, 1996). However, these yields are not achieved in practice. Average fresh-weight yields vary tremendously by country from 2 to 50 tonnes/ha with a global average of 16.7 tonnes/ha in 2007 (http://faostat.fao.org). Within large countries like China, with an average yield of 12.7 tonnes/ha, the variation from region to region can be nearly as great.

As potatoes cannot be grown all of the year round in most parts of the world, it is normal to have to store both seed tubers for planting the next crop and ware tubers for consumption. Hence, post-harvest infrastructure in terms of road transport and cold storage facilities is also an important aspect of successful potato production.

2 Origins and Domestication

2.1 Species Involved

The wild species progenitors of cultivated potatoes have been the subject of much discussion. Recently Spooner et al. (2005a) provided molecular taxonomic evidence for a single domestication in the highlands of southern Peru from the northern group of members of the *S. brevicaule* complex of diploid species. This group contains species such as *S. canasense*, *S. multidissectum*, and *S. bukasovii*, some of which are not always clearly resolved and perhaps could be better reduced to a single species, *S. bukasovii*. Sukhotu and Hosaka (2006) also concluded from chloroplast data that species such as these were first domesticated in Peru with a later spread to Bolivia. The result of domestication was a diploid cultigen *S. tuberosum* group Stenotomum (Dodds, 1962) from which all of the other cultivated potatoes were derived.

Dodds (1962) classified cultivated potatoes into five informal groups within one species *S. tuberosum* in which groups Andigena, Chaucha, Phureja, and Tuberosum were derived from group Stenotomum (Fig. 1.1). He also recognized two additional hybrid species involving wild species (*S.* × *curtilobum* and *S.* × *juzepczukii*) to which subsequent authors added *S.* × *ajanhuiri*, making eight groups in total. These eight groups are used in the rest of this chapter to avoid ambiguity. Hawkes (1990) gave groups Andigena and Tuberosum subspecies status and the other six groups, species status, making seven cultivated species in total. Spooner et al. (2007), using molecular data, have argued for four species. They regard frost-tolerant *S.* × *ajanhuiri* (diploid), frost-resistant *S.* × *juzepczukii* (triploid), and frost-resistant *S.* × *curtilobum* (pentaploid) as separate hybrid species derived from crosses between

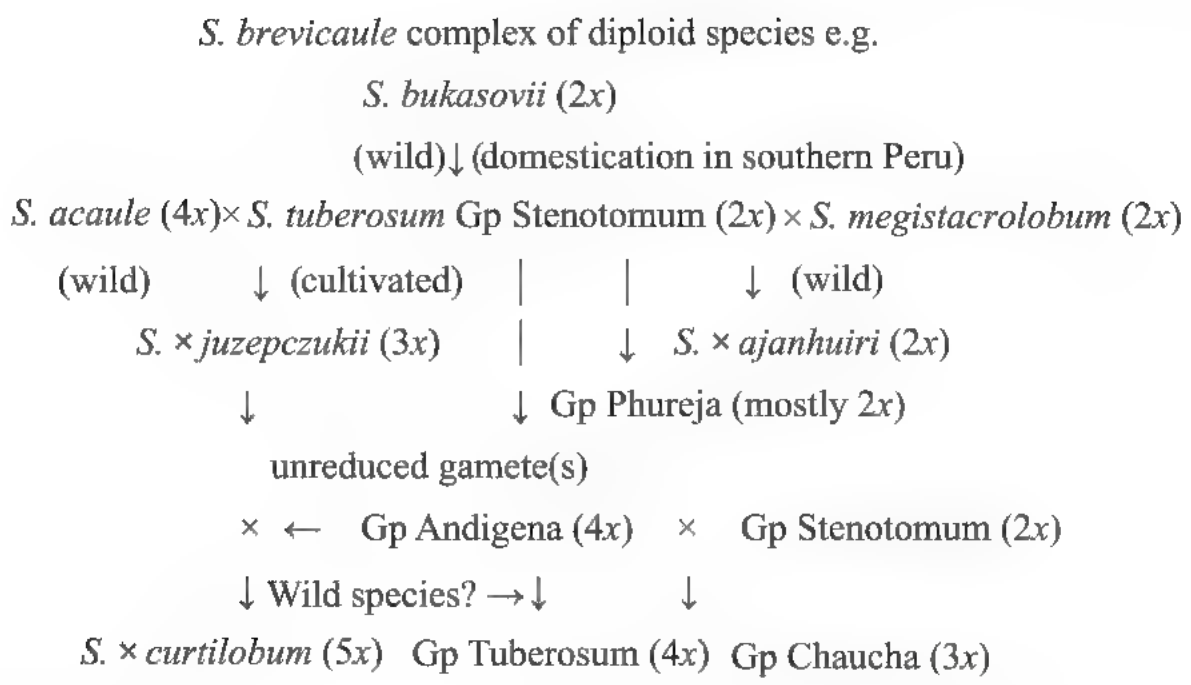
S. brevicaule complex of diploid species e.g.
S. bukasovii (2x)
(wild)↓ (domestication in southern Peru)
S. acaule (4x)× S. tuberosum Gp Stenotomum (2x) × S. megistacrolobum (2x)
(wild) ↓ (cultivated)
↓ (wild)
S. × juzepczukii (3x)
↓ S. × ajanhuiri (2x)
↓
↓ Gp Phureja (mostly 2x)
unreduced gamete(s)
× ← Gp Andigena (4x) × Gp Stenotomum (2x)
↓ Wild species? →↓ ↓
S. × curtilobum (5x) Gp Tuberosum (4x) Gp Chaucha (3x)

Fig. 1.1 Origin of cultivated groups of *S. tuberosum* (Dodds, 1962) and *S.* × *ajanhuiri*, *S.* × *juzepczukii* and *S.* × *curtilobum*, cultivated species with bitter taste and frost tolerance

domesticates and wild relatives. These 'bitter potatoes' are grown at high altitudes (up to 4,500 m for *S.* × *juzepczukii*) in the central Andes of Peru and Bolivia (Hawkes, 1990). *S.* × *ajanhuiri* is the hybrid of *S. tuberosum* group Stenotomum with the wild frost-resistant diploid species *S. megistacrolobum*, *S.* × *juzepczukii* is the hybrid of *S. tuberosum* group Stenotomum with the wild frost-resistant tetraploid species *S. acaule*, and *S.* × *curtilobum* is the hybrid between an unreduced gamete of triploid *S.* × *juzepczukii* and a normal gamete of *S. tuberosum* group Andigena. Spooner et al. (2007) regard groups Andigena, Chaucha, Phureja, Stenotomum, and Tuberosum (called by them Chilotanum) as a single species *S. tuberosum*, but now divided into two cultivar groups. These are the Andigenum group of upland Andean landraces containing diploids, triploids, and tetraploids, and the Chilotanum group of lowland tetraploid Chilean landraces. It is now useful to return to consider how these landraces arose.

First it is necessary to consider how group Andigena arose from group Stenotomum. Sukhotu and Hosaka (2006) concluded from chloroplast and nuclear DNA markers that group Andigena arose from group Stenotomum through sexual polyploidization from unreduced gametes many times at many places in the fields of group Stenotomum. These tetraploids were subsequently modified by occasional and unintentional selection of natural hybrids with neighboring wild species to give present-day group Andigena. Scurrah et al. (2008) have shown that closely related species growing around farmers' fields can hybridize with group Andigena and that some hybrid progeny would be selected by present-day Andean farmers. These results explain the chromosome behavior and tetrasomic inheritance of tetraploid *S. tuberosum* and why it can be regarded as the autotetraploid of diploid group Stenotomum for practical purposes. Hosaka (2004) suggested that Chilean Tuberosum (T) cytoplasm is derived from the southern wild species *S. tarijense* so that group Tuberosum is not simply group Andigena that has been selected to produce tubers in long days. Spooner et al. (2007) show that the T cytoplasm is also found at low frequency in Andean landraces including some diploids, indicating that the T cytoplasm moved northward as well as becoming predominant in Chilean

germplasm. However, this does not contradict the view that the Chilean landraces are secondarily derived from the Andean ones and that the long-day-adapted landraces of coastal Chile are genetically distinct from the short-day-adapted ones of the Andes (Raker and Spooner, 2002).

Returning to the other landraces, *S.* × *chaucha* is the triploid hybrid between diploid *S. tuberosum* group Stenotomum and tetraploid *S. tuberosum* group Andigena and, like group Stenotomum, is confined to the central Andes of Peru and Bolivia. In contrast, *S. tuberosum* group Phureja (diploid) was selected from group Stenotomum by Andean farmers for lack of tuber dormancy and faster tuber development so that they could grow up to three crops per year in the lower, warmer, eastern valleys of the Andes. Phureja potatoes were therefore able to spread into northern Ecuador, Colombia, and Venezuela and are the second most widely cultivated type in South America, after Andigena which is grown throughout the upland Andes of South America. Interestingly Ghislain et al. (2006) found that 32 out of 102 accessions of Phureja in the International Potato Center (CIP) collection of landraces were triploid or tetraploid, not diploid, in agreement with Hawkes (1990) that not all Phureja are diploid.

2.2 Reproductive Biology

The reproductive biology of potatoes is ideal for creating and maintaining variation. Potatoes, like their ancestral wild species, reproduce by sexual means and also by setting tubers. Potatoes flower and set true seed in berries following natural pollination by insects capable of buzz pollination, such as some bee species, which can release pollen from the poricidal anthers of potatoes (Scurrah et al., 2008). Outcrossing is enforced in cultivated (and most wild) diploid species by a single S-locus, multiallelic, gametophytic self-incompatibility system (Dodds, 1965). While self-incompatibility does not operate in tetraploid *S. tuberosum*, 40% (range 21–74%) natural cross-pollination was estimated to occur in group Andigena in the Andes (Brown, 1993) and 20% (range 14–30%) in an artificially constructed Andigena population (Glendinning, 1976). This sexual reproduction creates an abundance of diversity by recombining the variants of genes that arose by mutation, and potatoes are highly heterozygous individuals that display inbreeding depression on selfing. The genetically unique seedlings that grow from true seeds produce tubers that can be replanted as seed tubers and hence distinct clones can be established and maintained by asexual (vegetative) reproduction. Most potato cultivars are propagated through seed tubers and are genetically uniform. There are, however, circumstances where cultivars based on current methods of true potato seed (TPS) propagation are an attractive proposition despite being genetically variable and inferior to the best genotype that exists within the TPS progeny. These will be discussed in later sections. No doubt domestication occurred by human selection of tubers from naturally occurring variation, and the same was true for the subsequent farmer selection and propagation of landraces of potato.

2.3 History of Crop

The journey from gathering wild tubers to cultivating them and finally domesticating them started early in the human colonization of the Americas. Wild potato remains have been found in a late Pleistocene settlement in south central Chile dated around 12,500 years before present (Ugent et al., 1987; Moseley, 2001). Preserved food plant remains have been found at various excavated sites on the coast of Peru and one site in the high Chilca Canyon, south of Lima (Engel, 1970). The Oxford radiocarbon accelerator dated the tuber remains found by Engel to about 7,000 years before present. Fresh potatoes were most likely baked in the embers of a fire or cooked in an earth oven on hot stones (Hawkes, 1990). Lack of more evidence of cultivation in highland sites where the progenitor species are found probably simply indicates poor preservation conditions in high regions with seasonally wet climates, compared with better conditions in arid environments. Nevertheless, the extensive abandoned cultivation terraces throughout parts of the Andes suggest that potatoes were a very widespread crop in the Andes prior to the discovery of South America by the Spanish in 1533 (Hawkes, 1990) and remain so today. Interestingly, CIP (International Potato Center) are currently doing a project called PAPA ANDINA to develop a market chain for potatoes from small-scale growers in areas of rural poverty in Ecuador, Peru, and Bolivia to urban markets at home and abroad (Anderson, 2009).

2.3.1 Introduction to Europe

It is assumed that Pizarro and his men were the first Europeans to see potatoes being cultivated, in the Andes of Peru in 1533 during the Spanish conquest of the Incas, but there is no written record (Hawkes, 1990). In fact potatoes were first recorded in 1537 in what is now Colombia (Hawkes, 1990). The first record of cultivated potatoes outside of South America is their export in 1567 from Gran Canaria in the Canary Islands to Antwerp in Belgium (Hawkes and Francisco-Ortega, 1993). This was 6 years before they were first recorded in Spain in 1573 in the market archives of the Hospital de La Sangre in Seville (Hawkes and Francisco-Ortega, 1992). Potatoes were therefore probably first introduced from South America into the Canary Islands around 1562 and from there to mainland Europe (Hawkes and Francisco-Ortega, 1993).

The early introductions of potatoes to Europe included the one shown in the first water-color painting of a potato (late maturing, red skinned tubers of irregular shape with deep eyes) dated 1588 and the one shown in the first printed illustration (not as late in maturity, white skinned tubers of irregular shape with deep eyes) of 1597 (Hawkes, 1990). It has often been assumed that these early introductions came as ships' stores from Colombia and were of Columbian, or possibly Peruvian, origin and hence were primarily tetraploid group Andigena potatoes. Then as the growing of potatoes spread north-eastward across Europe, they became adapted to the long summer days of northern Europe and in this respect resembled Chilean potatoes. However, extant Canary Island potatoes comprise both Andean- and Chilean-type

landraces and Rios et al. (2007) have suggested that there were multiple early introductions of both types. Furthermore, they suggest that the early European potato was selected from the Chilean introductions because they were better adapted to European conditions. Potato introductions from South America were reviewed by Glendinning (1983), but one cannot say with certainty how many there were and what their contribution was to the subsequent spread of the potato in and from Europe, as reviewed by Hawkes (1990). It now seems safest to assume that the early introductions of cultivated potatoes to Europe came from both the Andes and coastal Chile (Hosaka et al., 1994; Spooner et al., 2005b; Rios et al., 2007). Analysis of DNA from 49 herbarium specimens has confirmed the presence of Andean potatoes from around 1700 and Chilean potatoes from 1811 in Europe (Ames and Spooner, 2008). Interestingly, molecular analyses of old Japanese cultivars were consistent with them being derived from group Andigena through early European potatoes (Hosaka et al., 1994) while recent molecular analyses have clustered all Indian potato varieties, including putatively remnant Andean populations, with Chilean Tuberosum (Spooner et al., 2005b).

2.3.2 Transition to Major Worldwide Food Crop

After their introduction to Europe, potatoes initially remained a botanic curiosity, being grown and studied in physic gardens for interest and medicinal purposes. Their potential as a food crop was first seen in Ireland at the end of the seventeenth century and throughout the eighteenth century (Burton, 1989). The climate and soil of Ireland proved suitable for potatoes but there were also societal and economic reasons for their increase in importance as a food crop. As a consequence, the population of Ireland increased in size from 2 million in 1700 to 8.5 million in 1845 (Reader, 2008). However, overreliance on the potato meant that the late blight epidemics of 1845 and 1846 resulted in famine in Ireland with profound societal consequences (Zadoks, 2008). Ironically, it was food shortages that proved to be the stimulus to potato cultivation throughout Europe during the eighteenth century because military and economic strength depended upon adequately fed manpower (Burton, 1989; Reader, 2008). Thus the eighteenth century saw potatoes accepted as a food throughout Europe and the nineteenth century saw their ascendancy as a major food crop (Burton, 1989), before a decline in potato production and consumption during the twentieth century. Globally, however, this decline was offset by what happened in the rest of the world.

During the seventeenth and eighteenth centuries many European countries developed widespread political and commercial interests in the rest of the world and the European (British, Dutch, French, Portuguese, and Spanish) colonists and missionaries took with them their common crops including potatoes (Burton, 1989; Pandey and Kaushik, 2003). Potato production expanded worldwide during the nineteenth century, but it was the expansion in China and India during the second half of the twentieth century that led to these countries becoming the first and third most important producers in the world.

3 Varietal Groups

The concept of varietal groups has not been used for potatoes. Nevertheless, some groupings have been found useful. As mentioned earlier, cultivated potatoes can be classified into five informal groups within *S. tuberosum* (groups Andigena, Chaucha, Phureja, Stenotomum, and Tuberosum) and three hybrids with wild species. Group Tuberosum is adapted to tuberization in long days, and this is understood. However, as a result of recent plant breeding, clarity is required when talking about long-day-adapted Andigena (Neotuberosum) and long-day-adapted Phureja potatoes. Otherwise, short-day adaptation will be assumed. It can also be useful to give an indication of adaptation to length of growing season by using maturity groups, a guide to days from planting to maturity and hence harvest date. In Britain there are first early (100–110 days), second early (110–120 days), early maincrop (120–130 days), maincrop (130–140 days), and late maincrop (140–150 days) varieties.

The World Catalogue of Potato Varieties 2009/2010 (Pieterse and Hils, 2009) provides information on the maturity, tuber shape, skin color, depth of eyes, flesh color, disease resistance, and use of varieties. Consumer preferences vary with country regarding skin (e.g., red, white, and russet) and flesh color, and varieties for different uses are also usually recognized. Furthermore, in characterizing Andean potato diversity, de Haan (2008) recognized three groups of cultivars for their roles in farming systems and household economies: native floury, native bitter, and improved or bred potatoes.

4 Genetic Resources

4.1 World Catalogue of Potato Varieties

The World Catalogue of Potato Varieties 2009/2010 (Pieterse and Hils, 2009) lists more than 4,500 varieties from 102 countries worldwide. Furthermore, a number of databases on modern cultivars are available, such as The European Cultivated Potato Database (http://www.europotato.org) which currently has information on 4,136 cultivated varieties. Google searches will find databases for many countries and organizations around the world. These modern cultivars provide breeders with parents adapted to their target environments, growing seasons, and end uses, but which require local evaluation and improvement.

4.2 Cultivated Potatoes in Latin America

Following its creation in Lima, Peru in 1970, The International Potato Center (CIP) (http://www.cipotato.org) assembled a collection of more than 15,000 accessions of potato cultivars (landraces) native to nine countries in Latin America: Argentina, Bolivia, Chile, Colombia, Ecuador, Guatemala, Mexico, Peru, and Venezuela.

Subsequently duplicate accessions were identified and the number of individual cultivars was reduced to 3,527 of which 552 were diploids, 128 triploids, 2,836 tetraploids (2,644 group Andigena, 144 group Tuberosum, and 48 hybrids), and 11 pentaploids (Huaman et al., 1997). By 1997 researchers at CIP had already conducted 46,124 evaluations on the collection for the reactions of cultivars to abiotic and biotic stresses and for other desirable traits. A core set of 306 group Andigena accessions was then established to aid utilization (Huaman et al., 2000a, b). They were chosen to represent the widest morphological diversity and to maximize geographical representation and hence should be valuable for future breeding both in South America and worldwide. The other genebanks mentioned below also have collections of cultivated species, but the one at CIP is recognized as the world collection. The collection is maintained by clonal propagation in the field and in vitro. In the future, cryopreservation may become an important component of maintaining clonal germplasm collections, thus allowing a reduction in the labor required for routine subculture of in vitro stocks. Much research has been done in recent years with some encouraging results that have been reviewed by Veilleux (2005).

4.3 Wild Tuber-Bearing *Solanum* Species

Wild tuber-bearing *Solanum* species are distributed from the southwestern USA (38°N) to central Argentina and adjacent Chile (41°S) (Hawkes, 1990; Spooner and Hijmans, 2001). They are a tremendous resource for potato breeding because of their wide geographical distribution and great range of ecological adaptation (Hawkes, 1994). In the southwestern USA and in Central America wild species generally occur at medium to high altitudes. In South America they are found along the Andes from Venezuela to northwest Argentina and also in the lowlands of Chile, Argentina, Uruguay, Paraguay, and southeastern Brazil. The adaptive range among the different species is very great and includes the high Andean regions from 3,000 m to the vegetational limit at 4,500 m where frosts are common, dry semi-desert conditions and scrub and cactus deserts, cool temperate pine and rain forests, and woodlands and coastal plains. Wild species have also developed resistances to a wide range of pests and diseases, but it is not clear if sources of resistance can be predicted from taxonomic and biogeographical variables. For example, Jansky et al. (2008) were unable to predict sources of early blight resistance.

There have been numerous collecting expeditions, from those pioneered by the Russians in the 1920s (Hawkes, 1990) to the more recent ones of the 1990s (Spooner and Hijmans, 2001). Reference books have been written on the potatoes of Argentina, Brazil, Paraguay and Uruguay (Hawkes and Hjerting, 1969), Bolivia (Hawkes and Hjerting, 1989; Ochoa, 1990), Peru (Ochoa, 2004), and North and Central America (Spooner et al., 2004). The collecting expeditions led to the establishment of a number of potato germplasm collections worldwide. The world collection is held at the CIP in Lima, Peru. The other main germplasm collections are the Commonwealth Potato Collection (CPC, Dundee, Scotland) (Fig. 1.2), the

Fig. 1.2 Part of the Commonwealth Potato Collection and cultivars Vales Everest (QTLs for resistance to white potato cyst nematode from group Andigena CPC 2802), Lady Balfour (QTLs for resistance to cyst nematodes from *S. vernei*), and Vales Sovereign (*H1* gene for resistance to golden potato cyst nematode from group Andigena CPC 1673) (Source: SCRI)

Dutch–German Potato Collection (CGN, Wageningen, The Netherlands), the Groß Lusewitz Potato Collection (GLKS, IPK, Groß Lusewitz, Germany), the Potato Collection of the Vavilov Institute (VIR, St. Petersburg, Russia), the US Potato Genebank (NRSP-6, Sturgeon Bay, USA), and Potato Collections in Argentina, Bolivia, Chile, Colombia, and Peru. Together they comprise the Association for Potato Intergenebank Collaboration and have established an Inter-genebank Potato Database (IPD) (www.potgenebank.org; or individual genebanks through Google). The IPD contains 7,112 different accessions of 188 taxa (species, subspecies, varieties, and forms) out of the 247 tuber-bearing wild potato taxa recognized by Hawkes (Huaman et al., 2000c). Accessions are normally held in true seed form. Data are available through the IPD links to individual collections for more than

33,000 evaluations of wild potato accessions covering 55 traits (dry matter, starch, reducing sugar and glycoalkaloid content, and resistances to fungi, bacteria, viruses, viroids, insects, and environmental stresses, such as frost and heat/drought).

The World Catalogue of Potato Varieties 2009/2010 (Pieterse and Hils, 2009) contains a 'Catalogue of the Global FAO-International Treaty "in trust" Wild Potato Collection at the International Potato Center (CIP).' The collection (CIP-genebank@cgiar.org) has 1,917 accessions and consists of representatives of 141 species with 67 from Peru, 29 from Bolivia, 13 from Mexico, 13 from Ecuador, and 10 from Argentina.

Some of the biological issues involved in the conservation of potato genetic resources have recently been discussed by Bamberg and del Rio (2005) along with the complicated issue of germplasm ownership. The International Treaty on Plant Genetic Resources for Food and Agriculture came into force on June 29, 2004, and was ratified by 55 countries (www.fao.org). It offers a multilateral system for easy access and exchange of germplasm in return for fair and equitable sharing of the benefits. Potatoes (section *Petota*, except *S. tuberosum* group Phureja) are one of the 35 food crops in the initial list covered by the multilateral system. It is too early to assess the impact of the treaty on the utilization of tuber-bearing *Solanum* species in potato breeding.

4.4 Taxonomy of Wild Tuber-Bearing *Solanum* Species

The taxonomy of wild tuber-bearing *Solanum* species is complicated and under continuous revision. Hawkes (1990) recognized 219 wild tuber-bearing species and arranged them into 19 series of subsection *Potatoe* of section *Petota* of subgenus *Potatoe* of genus *Solanum* (Table 1.1). He grouped series I–IX in superseries *Stellata* and series X–XIX in superseries *Rotata*. He considered the sequence of subsections, superseries, and series to reflect an approximate evolutionary one and suggested a possible scenario for the evolution of wild potato species. He postulated that (diploid) wild potatoes originated in Mexico and expanded to South America, from where a newly evolved group returned to North America. However, distributional and ploidy data suggest a South American origin (Hijmans et al., 2007), so the matter remains unresolved. Hawkes also recognized a further nine closely related non-tuber-bearing species that he grouped into two series of subsection *Estolonifera*, but these have been excluded from section *Petota* in more recent taxonomic reviews, leaving a section comprising all tuber-bearing species.

The latest summary by Spooner and Salas (2006) recognizes 188 wild potato species for section *Petota* that are grouped into four clades, based on plastid DNA, rather than 19 series (Table 1.1). Clade 1 comprises the US, Mexican, and Central American diploid species, exclusive of *S. bulbocastanum*, *S. cardiophyllum*, and *S. verrucosum*; Clade 2 comprises *S. bulbocastanum* and *S. cardiophyllum*; Clade 3 comprises all examined members of the South American series *Piurana* and some South American species classified into other series; and Clade 4 comprises

Table 1.1 Classification of wild tuber-bearing *Solanum* species (Section *Petota*) based on Hawkes (1990) and Spooner and Salas (2006) and species mentioned in text

Superseries	Series	Species numbers	Ploidy	EBN	Area[a]	Plastid clade
Superseries *Stellata*						
I	*Morelliformia*	1	2*x*	1	Mex	1
II	*Bulbocastana*	2	2*x*	1	Mex	1
	S. bulbocastanum		2*x*	1	Mex	2
III	*Pinnatisecta*	11	2*x*	1	Mex	1
	S. cardiophyllum		2*x*	1	Mex	2
IV	*Polyadenia*	2	2*x*	1	Mex	1
V	*Commersoniana*	2	2*x*	1	SA	4
VI	*Circaeifolia*	3	2*x*	1	SA	4
VII	*Lignicaulia*	1	2*x*	1	SA	4
VIII	*Olmosiana*	1	2*x*	1	SA	4
IX	*Yungasensa*	9	2*x*	2	SA	4
	S. chacoense		2*x*	2	SA	4
Superseries *Rotata*						
X	*Megistacroloba*	11	2*x*	2	SA	4
	S. megistacrolobum		2*x*	2	SA	4
	S. raphanifolium		2*x*	2	SA	4
XI	*Cuneoalata*	3	2*x*	2	SA	4
XII	*Conicibaccata*	40	2*x*, 4*x*, 6*x*	2,2,4	SA, Mex	4
XIII	*Piurana*	15	2*x*, 4*x*	2	SA	3
XIV	*Ingifolia*	2	2*x*	2	SA	4
XV	*Maglia*	1	2*x*	2	SA	4
XVI	*Tuberosa*	96	2*x*, 4*x*	2	SA	4
	S. brevicaule		2*x*	2	SA	4
	S. bukasovii		2*x*	2	SA	4
	S. canasense		2*x*	2	SA	4
	S. leptophyes		2*x*	2	SA	4
	S. multidissectum		2*x*	2	SA	4
	S. sparsipilum		2*x*	2	SA	4
	S. spegazzinii		2*x*	2	SA	4
	S. vernei		2*x*	2	SA	4
	S. verrucosum		2*x*	2	Mex	4
XVII	*Acaulia*	4	4*x*, 6*x*	2,4	SA	4
	S. acaule		4*x*	2	SA	4
XVIII	*Longipedicellata*	7	4*x*	2	Mex	4
	S. stoloniferum		4*x*	2	Mex	4
XIX	*Demissa*	8	6*x*	4	Mex	4
	S. demissum		6*x*	4	Mex	4

[a]SA = South America; Mex = Southwestern USA, Mexico, and Central America.

all remaining South American species (including cultivated potatoes) and the US, Mexican, and Central American polyploid species and *S. verrucosum*. However, this plastid-based classification splits similar species into different clades and so may not properly represent groupings made on the basis of nuclear DNA. Furthermore, it is not an appropriate means of classifying allopolyploid groups. The number of species

may be further reduced in the future, and clade composition based on chloroplast DNA may change as extensive nuclear DNA sequence data become available. Of more interest to potato breeders is the origin and relatedness of the genomes in wild and cultivated potatoes, including hybrid taxa, and their accessibility for breeding via crossing.

The wild species form a polyploid series from diploid ($2n = 2x = 24$) to hexaploid ($2n = 6x = 72$) in which only diploid cytotypes have been found in 123 species and only polyploids in 43 species (Hijmans et al., 2007). There is some evidence that polyploidy played an important role in the environmental differentiation and range expansion of wild potatoes (Hijmans et al., 2007). The two most widespread species are both tetraploids, *S. stoloniferum* in North and Central America and *S. acaule* in South America. Genomes were classified into five groups A, B, C, D, and P by Matsubayashi (1991), with a sixth group E recognized in closely related non-tuber-bearing species. Spooner et al. (2004) summarized the putative genome compositions of the polyploid species, but it is clear that further research is required to resolve their origins. For example, recent data support *S. bulbocastanum* (Wang et al., 2008) and *S. verrucosum* (Pendinen et al., 2008) as the progenitors of the allotetraploid *S. stoloniferum*. Nearly all of the diploid species are outbreeders, with a single S-locus, multiallelic, gametophytic self-incompatibility system (Dodds, 1965), whereas the tetraploids and hexaploids are mostly self-compatible allopolyploids that display disomic inheritance (Hawkes, 1990). A dominant self-incompatibility inhibitor has been found in *S. chacoense* (Hosaka and Hanneman, 1998) and used in breeding, just as one had previously been found in a dihaploid (see below) of *S. tuberosum* (De Jong and Rowe, 1971).

4.5 Crossability of Species

The crossability of species has been determined through artificial pollinations done across many years (Jansky, 2006). The results can be explained primarily but not exclusively in terms of endosperm balance number (EBN), which can be regarded as the effective rather than the actual ploidy of the species (Johnston et al., 1980). In crosses between species with the same EBN the hybrids have a normal endosperm for nourishing the hybrid embryo, whereas in crosses between species with different EBNs the endosperm degenerates. The endosperm develops following the fusion of a sperm nucleus from the male parent with two polar nuclei from the female parent to give a triple fusion nucleus and it is the genetic composition of this nucleus that is important. Under the EBN hypothesis the endosperm is normal when the three nuclei have the same EBN and hence a 2 maternal to 1 paternal ratio of endosperm balance factors. Attempts have been made to understand the genetic and biological basis of the EBN concept, but EBNs are determined experimentally relative to species assigned an arbitrary value of 1 (Hermsen, 1994). The main groups of species are diploid EBN = 1, diploid EBN = 2, tetraploid EBN = 2, tetraploid EBN = 4 (including *S. tuberosum*), and hexaploid EBN = 4 (Hawkes and Jackson,

1992). Species within these crossability groups have evolved by means of geographical and ecological isolation rather than by genetic incompatibility and hybridizations are usually successful.

Today breeders can usually achieve sexual hybridization between *S. tuberosum* and its wild relatives by manipulation of ploidy with due regard to EBN (Ortiz, 1998, 2001; Jansky, 2006). EBN can be doubled meiotically through the unreduced 2*n* gametes produced from several naturally occurring recessive meiotic mutations that are common in *Solanum* species (Tai, 1994; Jansky, 2009). It can also be doubled mitotically through the use of colchicine for chromosome doubling, something which can also occur naturally during callus culture. In fact, Stupar et al. (2007) were able to produce diploid and tetraploid regenerants when somatic leaf cells from their monoploid were exposed to leaf disk regeneration. EBN can be halved by haploidization using in vitro androgenesis (anther culture) or more commonly in *S. tuberosum* by parthenogenesis using pollinations with particular clones of diploid group *phureja* (Wenzel, 1994; Veilleux, 2005). Furthermore, embryo rescue can be used to secure a hybrid where embryo abortion is due to a defective endosperm (Hermsen, 1994; Jansky, 2006). As the largest compatibility group is EBN = 2, it is now common for potato breeders to secure tetraploid hybrids from 4*x* (*S. tuberosum*) × 2*x* (2*x S. tuberosum* × wild species) crosses in which an unbalanced endosperm prevents the development of triploid embryos. There are, however, other barriers to hybridization, such as interspecific pollen–pistil incompatibility and nuclear-cytoplasmic male sterility, although fertility restorer genes have been found for the latter (Jansky, 2009). Unilateral incompatibility is known to occur when a self-incompatible (SI) species is pollinated by a self-compatible (SC) one so that *S. verrucosum* (SC female) × *S. phureja* (SI male) is successful, but the reciprocal cross fails (Hermsen, 1994; Jansky, 2006). Sometimes incompatible pollen can be helped to achieve fertilization through a second pollination with compatible pollen, a technique known as mentor pollination (Hermsen, 1994; Jansky, 2006). These phenomena have been reviewed by Camadro et al. (2004) in the context of how sympatric species maintain their integrity. From time to time potato breeders have unexpected successes and failures when attempting to overcome barriers to hybridization.

Potato breeders can also use somatic (protoplast) fusion to achieve difficult or impossible sexual hybridizations and in ploidy manipulation to achieve maximum heterozygosity (Wenzel, 1994; Thieme and Thieme, 2005; Veilleux, 2005). Protoplast fusion can be induced chemically by the polycation polyethyleneglycol (PEG) or via electrofusion that is now the preferred method. Somatic hybrids derived from the same fusion combination do show genotypic and phenotypic variation and hence require screening for the desired product. Somatic fusion has allowed the production of fertile hexaploid hybrids between tetraploid *S. tuberosum* (EBN = 4) and diploid EBN = 1 species, such as the non-tuber-bearing species *S. brevidens* that has tuber soft rot and early blight resistances (Tek et al., 2004) and *S. bulbocastanum* that has a major gene for broad spectrum resistance to late blight (Naess et al., 2000). Somatic fusion has also allowed the production of diploid hybrids from monoploids of group Tuberosum and group Phureja (Lightbourn and Veilleux, 2007) and tetraploid hybrids from dihaploids (the haploids produced from 4*x*

S. tuberosum), including male-sterile ones (Thieme and Thieme, 2005). Dominant resistance genes as well as quantitative traits can be combined in the same way as when gametes fuse in sexual hybridization.

5 Major Breeding Achievements

5.1 In South America Following Domestication

It is assumed that domestication involved selection for less bitter and hence less toxic tubers, but interestingly Johns and Alonso (1990) found that some genebank accessions of *S. bukasovii* had tuber glycoalkaloid levels which were consistently close to the levels found in many clones of *S. tuberosum* group Stenotomum. They concluded that exploitation and domestication of this species would have required little or no selection for lower glycoalkaloid level, unlike their samples of *S. canasense*, *S. leptophyes*, and *S. sparsipilum*. Nevertheless, it seems fair to credit Andean farmers with making the potato an edible crop.

Andean farmers certainly retained a much wider variety of tuber shapes and skin and flesh colors than is seen in wild species (Simmonds, 1995), and this diversity can only have arisen by mutation under domestication. Furthermore, naturally occurring tetraploid types of potato came to be selected in preference to their diploid ancestors, presumably because farmers found them superior for yield and other traits. Subsequent selection for appropriate maturity and dormancy, higher yields and harvest index, and resistance to abiotic and biotic stresses must have occurred in many environments. Stupar et al. (2007) developed a synthetic autopolyploid series in potato (primarily group Phureja) that included one monoploid ($1x$) clone, two diploid ($2x$) clones, and one tetraploid ($4x$) clone, in order to explore phenotypic and transcriptomic (about 9,000 genes) changes associated with autopolyploidization. Interestingly, the diploid plants were the most vigorous and generated the greatest biomass with the monoploid inferior to both the diploids and the tetraploid. However, the diploid and tetraploid plants had similar gene expression patterns. Therefore the eventual superiority of tetraploid potatoes probably resulted from them exploiting their increased potential for heterozygosity rather than polyploidy per se.

The original CIP collection of more than 15,000 accessions of potato cultivars (landraces) native to nine countries in Latin America (Argentina, Bolivia, Chile, Colombia, Ecuador, Guatemala, Mexico, Peru, and Venezuela) is testament to the achievements of the farmers of these countries.

5.2 Modern Potato Breeding

Modern potato breeding began in 1807 in England when Knight made the first recorded hybridizations between varieties by artificial pollination (Knight, 1807),

although named cultivars can be traced to the 1730s (Reader, 2008). It flourished in Europe and North America during the second half of the nineteenth century when exchanges of germplasm started to occur and many new cultivars were produced by farmers, hobby breeders, and seedsmen. Even then, the raising of seedlings from seed of self-set berries remained a common practice which continued into the twentieth century. North America's most popular potato cultivar, Russet Burbank, released in 1914, was descended from Rough Purple Chili through three generations of open pollination (Ortiz, 2001). Modern potato breeding in India and China started later in the 1930s, but with rapid expansion since 1948 and 1978, respectively (Gaur et al., 2000; Jin et al., 2004).

The extent of progress since 1807 can be judged by the latest World Catalogue of Potato Varieties (Pieterse and Hils, 2009) which lists more than 4,500 varieties from 102 countries covering all potato growing regions in the world. Although a much smaller number have been widely grown, this is nevertheless a remarkable achievement for a crop which was unknown outside of South America until almost 500 years ago and which was derived from a narrow genetic base. It represents adaptation of the potato to the wide range of environments and end uses mentioned in the Introduction. The initial adaptation of potatoes to growing in long days must have resulted in dramatic increases in yield. Then during the twentieth century in Europe and North America, yields more than doubled in some countries with increases in Great Britain (GB) from 22 to 45 tonnes/ha over the period 1960–2003 (British Potato Council statistics) and likewise in the USA from 5.6 to 33.6 tonnes/ha over the period 1920–1989 (Lucier et al., 1990). However, the contribution of new cultivars to the yield increases appears to have differed in GB and the USA. Simmonds (1981) provided evidence of a 5.5 tonnes/ha increase in GB from the near replacement of cultivars 'King Edward' and 'Majestic' with three more modern cultivars 'Pentland Crown,' 'Maris Piper,' and 'Desiree.' In contrast, Douches et al. (1996) in the USA found a lack of improvement in yield and specific gravity when cultivars released over the period 1861–1991 were compared for 3 years in a high-yielding environment (50 tonnes/ha), but they did find trends to earlier maturity and improved tuber appearance. Furthermore, Love et al. (1998) provided evidence of significant progress since 1960 in North America in developing cultivars with good processing quality.

5.3 Introgression of Genes from Wild and Cultivated Species

In 1908 in Germany and 1909 in GB, recognition of *S. demissum* as a source of genes for resistance to late blight marked the start of introgression breeding (Muller and Black, 1951). Resistance to late blight was introgressed from *S. demissum* and *S. stoloniferum*, resistance to viruses from these species together with *S. chacoense* and *S. acaule*, and resistance to potato cyst nematodes from *S. vernei* and *S. spegazzinii*. By the end of the 1980s these wild species, together

with cultivated *S. tuberosum* groups Andigena and Phureja, had been used extensively in the breeding of successful cultivars in Europe (Ross, 1986). Likewise the species *S. demissum*, *S. chacoense*, and *S. acaule* were used extensively in North America (Plaisted and Hoopes, 1989), and one of the most successful cultivars to be introduced into China by CIP, CIP-24, or Achirana-INTA, bred by the Instituto Nacional de Tecnología Agropecuaria, Argentina, had *S. acaule*, *S. demissum*, and *S. stoloniferum* in its pedigree (Ortiz, 2001). Nevertheless, the introgression of genes from wild and cultivated species has been fairly limited in number but is expected to increase.

The resistances to viruses and cyst nematodes (Fig. 1.2) proved valuable in crop production, whereas the *S. demissum*-derived R genes failed to provide durable resistance to late blight either singly or in combination due to the evolution of new races of *Phytophthora infestans* (Malcolmson, 1969). Breeders therefore switched to selection for high levels of quantitative field resistance, either by using races of *P. infestans* compatible with the R genes present in their material or by creating R gene-free germplasm so that screening could be done with any race (Toxopeus, 1964; Black, 1970; Wastie, 1991; Ortiz, 2001). Results have been mixed and the most widely grown cultivars today are still usually susceptible to late blight (Forbes et al., 2009). Currently there is much debate over whether or not the R genes for blight resistance being found in other wild species will be more durable per se or can be deployed in a more durable way (Goverse and Struik, 2009).

5.4 Introgression and Base Broadening

Peloquin and his coworkers (Hermundstad and Peloquin, 1987; Jansky et al., 1990) developed a novel breeding strategy to introgress specific characteristics and to broaden the genetic base of potato in a way similar to that envisaged by Chase (1963) in his analytic breeding scheme. This strategy was made possible by the production of haploids (also called dihaploids) of *S. tuberosum* from 1958 onward (Hougas et al., 1958). The hybrids between haploids of *S. tuberosum* and diploid wild species with an EBN of 2 will often form tubers in long-day growing conditions (Jansky et al., 2004; Jansky, 2009). When they also produce $2n$ gametes by FDR (first division restitution), much of the genetic diversity of the wild species can be efficiently transferred to the tetraploid offspring from $4x \times 2x$ crosses and results in about 25% of the wild species genes in the final product (Tai, 1994; Jansky, 2009). Tai (1994) concluded, however, that haploid-wild species hybrids need to be improved before they are used in $4x \times 2x$ crosses, for example, through population improvement by recurrent selection (Rousselle-Bourgeois and Rousselle, 1992). In contrast, diploid hybrids with *S. raphanifolium* with resistance to cold-sweetening after storage for 3 months at 2°C have been used by Hamernik et al. (2009) to produce commercially acceptable tetraploid offspring without extensive backcrossing to cultivated germplasm. These should be valuable parents for producing new cultivars suitable for processing.

5.5 Base Broadening

During the second half of the twentieth century recognition was given to the value of the cultivated species of South America for broadening the genetic base of European and North American breeding programs. Breeding experiments in Europe and North America demonstrated that through simple mass selection under northern latitude, long-day summer conditions, group Andigena will adapt and produce parents suitable for direct incorporation into European and North American potato breeding programs (Glendinning, 1975; Munoz and Plaisted, 1981). Neotuberosum germplasm provided adapted sources of resistance to important pathogens including *Globodera rostochiensis* (golden potato cyst nematode) and *Potato virus Y* (PVY) (Plaisted, 1987). Likewise, Carroll (1982) (Fig. 1.3) and Haynes (Haynes and Lu, 2005) produced populations of group Phureja/group Stenotomum adapted to long-day conditions in Europe and North America, respectively. Direct hybridization of Carroll's improved diploid population with tetraploid potato cultivars via unreduced pollen grains ($4x \times 2x$ crosses) resulted in tetraploid hybrids, some of which were superior to standard tetraploid cultivars in both total and marketable yields (Carroll and De Maine, 1989). Furthermore, diploid cultivars, such as Mayan Gold, have now been produced from this population, but they are targeted at niche markets

Fig. 1.3 Long-day-adapted group Phureja potatoes from the population of Carroll (1982) (Source: SCRI)

because their yield is only two-thirds that of Tuberosum potatoes. Despite these breeding efforts, relatively few clones of Neotuberosum (long-day group Andigena) and long-day group Phureja/group Stenotomum have been used to any extent in the breeding of modern cultivars. Part of the reason for this is that while adaptation to tuberization in long days was quickly achieved, other problems remained. Neotuberosum clones lacked the regularity of tuber shape of intensively selected group Tuberosum clones and long-day-adapted group Phureja clones lacked tuber dormancy. Hence these populations need to be selected for further improvements to achieve the original goal of their direct use as parents in breeding finished cultivars for European and North American markets.

CIP on its establishment recognized the need to make broad-based germplasm and candidate varieties from the world collection available to National Programs in developing countries, particularly germplasm with durable resistance to late blight. Probably the best-known broad-based germplasm from CIP's breeders is Population B with quantitative resistance to late blight. The aim was to help with the development of improved cultivars, for a wide range of environments, which possessed high and stable levels of resistance to late blight in combination with resistances to viruses and suitable tuber type, and culinary and processing quality (Trognitz et al., 2001; Landeo, 2002). The population improvement involved recurrent selection for quantitative resistance to late blight and other desirable traits under high endemic disease pressure in the Andean highlands together with selection in those geographical areas where the new cultivars were to be grown, for example, in short days in East Africa (Mulema et al., 2004). Evaluation under long days in Argentina (Trognitz et al., 2001) and in South Korea was included to broaden the range of adaptation of the largely short-day-adapted population. Clones with good general combining ability have been identified for use as parents in the local breeding programs of the National Agricultural Research Systems in developing countries. Landeo (2002) and Landeo et al. (2007) reported good progress in selecting for resistance and other traits in Population B, large additive genetic variances and high heritability estimates for resistance, and stability of resistance across diverse environments and pathogen populations in tropical environments.

Parallel efforts at CIP have developed the lowland tropic virus-resistant population denoted as LTVR. This population combines the heat tolerance and early bulking ability of *S. tuberosum* germplasm bred under the summer conditions of the Northern Hemisphere on the one hand, with virus resistance from native *S. tuberosum* group Andigena and Neotuberosum on the other. Recurrent selection with evaluations in a range of environments on the Peruvian coast led to the development of multiplex progenitors of extreme resistance to PVY and PVX, and the selection of virus-resistant clones better adapted to the warm conditions of the lowland tropics in each selection cycle. More recently, advanced germplasm from European and other long-day breeding programs was incorporated to improve resistance to *Potato leafroll virus* (PLRV), while enhancing earliness and market traits.

In the Central Potato Research Institute of India there has been interest in Tuberosum (female) × short-day Andigena hybrids in breeding for the sub-tropical plains where the potato crop is grown under short days (Gopal et al., 2000; Kumar

and Kang, 2006). A number of Indian potato cultivars have already been developed from Tuberosum × Andigena crosses, including 'Kufri Pukhraj,' 'Kufri Giriraj,' 'Kufri Chipsona II,' and 'Kufri Shailja' (Kumar et al., 2008).

5.6 TPS

Most potato cultivars are clonally (vegetatively) propagated through seed (daughter) tubers and are genetically uniform. There are, however, circumstances where cultivars based on current methods of true potato seed (TPS) propagation are an attractive proposition despite being genetically variable. Breeding cultivars for TPS was started at CIP in 1972 with the aim of high yields and acceptable uniformity. Methods and progress have been reviewed by Golmirzaie et al. (1994) and Ortiz (1997). TPS propagation appeared most attractive in the torrid zones of the lowland tropics and subtropics. Here the difficulty of establishing a TPS crop, later maturation, and less uniformity could be outweighed by three advantages (Golmirzaie et al., 1994). Seed costs are reduced due to the much smaller amounts of planting material required. Planting time is flexible because the farmer does not have to consider the physiological age and condition of seed tubers. Finally, tubers are free from tuber-borne diseases with the possible exception of the few caused by true seed-borne viruses. In practice TPS potatoes have been established in Bangladesh, China, Egypt, India, Indonesia, Nicaragua, Peru, Philippines, southern Italy, and Vietnam (Almekinders et al., 1996; Ortiz, 1997; Simmonds, 1997). They have proved extremely useful for food security, particularly for small-scale farmers (Chujoy and Cabello, 2009). Chilver et al. (2005) have recently reviewed on-farm profitability and prospects for TPS and concluded that widespread geographic adoption is unlikely in the immediate future, but that investment in a small but sustained TPS breeding effort can be justified in both China and India.

5.7 Somaclonal Variation and Mutation Breeding

Somaclonal variation can occur when plant regeneration and multiplication involves tissue culture, particularly when there is a callus phase. After such variation was first reported in protoclones of cultivar Russet Burbank (Shepard et al., 1980), it was investigated as a breeding method in its own right. Desirable improvements on parent cultivars were reported and assessed under field conditions, but most somaclonal variations comprised undesirable changes that did not merit further breeding effort (Kumar, 1994; Veilleux, 2005). Hence today somaclonal variation tends to be viewed as a source of undesirable variants that need to be screened out of breeding programs that involve plant regeneration.

Likewise, although natural mutations are the ultimate source of all genetic variations, the potato is not ideal for deliberate mutation breeding because it is a clonally

propagated tetraploid crop. Nevertheless, limited success has been achieved, for example, selecting gamma-ray mutants of the cultivar Lemhi Russet for improved resistance to blackspot bruise and low-temperature sweetening (Love et al., 1993).

5.8 Genetic Transformation

Potato transformation using *Agrobacterium*-mediated systems was developed during the 1980s, first with *A. rhizogenes* (Ooms et al., 1986) and then more successfully with *A. tumefaciens* (Stiekema et al., 1988; Dale and Hampson, 1995). The gene of interest would be incorporated into the bacterial plasmid along with a promoter and selectable marker, such as resistance to an antibiotic or herbicide; the bacterium would be co-cultured with freshly cut tuber discs or leaf or internode explants of the potato; and regeneration of shoots with the selectable marker would take place in plant tissue culture in the presence of the selectable agent. Recently both Chang et al. (2002) and Morris et al. (2006) have been able to simultaneously co-transform potatoes with two genes using a single selectable marker. The transgene constructs were multiplied separately in *A. tumefaciens* clones, and cultures of the *Agrobacterium* were mixed and incubated with the potato internode explants. From 300 explants, Morris et al. (2006) generated 38 independent transformants of which four contained both transgenes. Clearly this increases the speed and efficiency of transformation as a breeding method and makes it a more attractive proposition. The choice of promoter is important for gene expression. The CaMV 35S promoter has frequently been used for constitutive gene expression, but others have been developed for higher constitutive expression and for leaf or tuber expression (Douche and Grafius, 2005).

Monsanto was the first to commercialize GM potatoes in North America from 1995. The GM cultivars were Russet Burbank, Atlantic, Snowden, and Superior with a *Bt* gene for pest resistance from the bacterium *Bacillus thuringiensis*. Subsequently virus resistance was added (Davies, 2002). Trait stability was demonstrated in field trials across a number of years, as was the greatly reduced use of pesticides (Duncan et al., 2002). But leading processing and fast food outlet companies in North America were reluctant to purchase GM potatoes, because of consumer concerns over GM potato products, and Monsanto stopped marketing GM potatoes in 2001. There has also been resistance to GM potatoes in the European Union. The first GM potato for non-food use to be cultivated in Europe is likely to be Amflora, a pure amylopectin starch potato developed by BASF Plant Science by switching off the gene for the granule-bound starch synthase (GBSS), the key enzyme for the synthesis of amylose. However, in 2009 there were still delays in its approval for commercial production because of concerns over the antibiotic resistance marker which it contains. The first GM potatoes for human consumption in Europe and North America are likely to come from recent advances in producing marker-free transformants and from new cisgenic and intragenic approaches (see Section 7.5).

6 Current Goals of Breeding

6.1 Asia, Africa, and Latin America

In Asia, Africa, and Latin America there is a need for increased potato production to meet increasing demands for food from human population growth and thus achieve food security. Both China and India are planning large increases in production by increasing the area under cultivation, with India also projecting increases in yield (Anderson, 2009). Interestingly, however, if China could markedly increase its area of potatoes planted with healthy seed from the current 20%, and effectively control late blight, bacterial wilt, and viruses, the yield per hectare would be expected to double (Anderson, 2009). This brings home the point that new cultivars with inbuilt resistance to these and other diseases and pests are highly desirable. Furthermore, selection for higher and stable yields would also be worthwhile but should take place in environments with appropriate inputs of fertilizers and water, otherwise genotype × environment interactions might prevent yield increases being realized in farmers' fields. Expansion of potato growing into a wider range of environments might require adaptation to changes in the growing season (planting time and length of season) and resistance to abiotic stresses could become important. These include drought, heat, cold, mineral deficiency, and salinity, with water stress being the most important one that affects potato production in most areas of the world. If intercropping increases in warm climates, then shade crops (e.g., sugarcane in India) could help to reduce heat stress in potatoes, but heat-tolerant cultivars are still desirable.

Although the potato is a wholesome food, further improvements in its nutritional and health properties are worth considering. There is current interest in improving the health of poor people by breeding staple foods that are rich in micronutrients (biofortification). CIP has already found accessions in its germplasm collections with higher contents of iron and zinc (Burgos et al., 2007). In vitro assays have also shown variation among potato genotypes in the bioavailability of Fe, and that in particular, the consumption of yellow-fleshed potatoes, which are generally higher in carotenoid contents than white or cream-fleshed potatoes, may enhance the bioavailability of Fe from other sources in the diet. While heritability of carotenoid concentrations in potato has not been determined, the heritabilities of Fe concentration and vitamin C, which also enhances bioavailability, are moderately high, indicating that breeding for increased bioavailable Fe in potato is feasible.

Furthermore, higher beta-carotene (vitamin A) content is now a realistic target for potato given recent success in modifying carotenoid biosynthesis through genetic transformation (Ducreux et al., 2005), and increased protein content and better amino acid balance have been achieved through transformation with a non-allergenic seed albumin gene (*AmA1*) from *Amaranthus hypochondriacus* (Chakraborty et al., 2000). Finally, as mentioned in the Introduction, processors are building factories in countries where the potato is primarily grown as a staple food, and this is a trend that is likely to continue. In these circumstances there is going to be a need for new locally adapted cultivars that meet the stringent requirements

of processors. Appropriate tuber morphology and texture, adequate solids, and low reducing sugar content are important as well as freedom from mechanical damage, bruising, and internal defects.

6.2 Europe, North America, and Oceania

In Europe, North America, and Oceania, food security has been achieved and a number of countries have yields in excess of 40 tonnes/ha. The emphasis is on trying to increase potato usage in an economically and environmentally sustainable way. New cultivars are required which give more yield of saleable product at less cost of production, whether the potatoes are for processing or table use. However, in the European Union, for example, there is political pressure for reduced use of pesticides and fungicides and better use of water and fertilizers, both nitrogen and phosphate, all resources required to achieve high potato yields and quality. Hence, new cultivars are required to meet these objectives together with the quality ones demanded by processors and supermarkets. Finally, there is a need for new cultivars to meet consumer demands for convenience foods and novel products, preferably with improved texture and flavor and health-promoting attributes. Processors are currently under pressure to reduce acrylamide formation in crisps (chips) and French fries because of concerns about its effects on human health (Amrein et al., 2003; Pedreschi, 2009; Pinhero et al., 2009). As acrylamide is formed in processed potato products by Maillard browning reactions between reducing sugars and the amino acid asparagine, lower levels of these compounds are obvious targets for conventional breeding and genetic engineering. Cultivars with a low GI could be of value in lowering the glycemic load of the western diet, thus decreasing the risk of type-2 diabetes, cardiovascular disease, and obesity (Storey, 2007). For example, following cooking, a portion of high amylose starch recrystallizes to form so-called resistant starch, which acts as a form of dietary fiber (Karlsson et al., 2007). The introduction of inulin to potato is another way of improving its nutritional value by reducing its energy density through increased dietary fiber. Hellwege et al. (2000) have developed transgenic potato tubers that synthesize the full range of inulin molecules naturally occurring in globe artichoke (*Cynara scolymus*).

In countries with a starch industry there are considerable opportunities to breed or genetically engineer potatoes with novel starches for use in food and non-food products. Potato starch has numerous useful functional properties such as thickening, coating, gelling, adhesion, and encapsulation. Some of these functionalities are unique to the polymer as a result of the structure and organization of its linear amylose (17–25% of starch) and highly branched amylopectin (Li et al., 2006). Genetic engineering has already generated the two extreme types of potato starch. High amylopectin starch was produced by the down-regulation of the granule-bound starch synthase gene that controls amylose synthesis (Visser et al., 1991) and high amylose starch by concurrently down-regulating two starch branching enzymes, A and B (Schwall et al., 2000).

6.3 Climate Change

Haverkort and Verhagen (2008) reviewed the likely consequences of climate change on potato production based on the International Panel on Climate Change report (IPCC, 2007). Climate change will bring a rise in temperature, an increase in carbon dioxide concentration in the air, and an altered precipitation pattern. In parts of the world such as the Mediterranean and Sahelian Africa, potato yields will go down as the suitable heat-free period of the year for production becomes shorter. In these areas breeding for heat tolerance will be important because of the adverse effect of high temperatures on tuberization. Furthermore, with a higher evaporative demand, water will be used less efficiently and breeding for drought tolerance will also be important. In contrast, potato yields in temperate climates may increase due to higher carbon dioxide concentrations in the air and a longer growing season. In northern Europe, there will be a decreasing number of days with frost, more rain in winter and less in summer, with more erratic but heavier rain storms. Water availability for irrigation will be important to maintain yields and quality.

Throughout the world then, there is a drive for cultivars that make better use of water, and either avoid drought (faster tuber bulking) or are tolerant of drought. Not surprisingly, there is increased research on root architecture (Iwama, 2008), looking at the effects of variation on water use and the correlation between field and glasshouse screens. Furthermore, effects of root architecture on fertilizer use cannot be ignored. Potatoes need large inputs of phosphate fertilizer, compared with other crops, and in Europe, for example, most potato growing is in nitrate vulnerable zones.

Climate change is also likely to bring new challenges in reducing losses from pests and diseases. Higher temperatures and longer growing seasons are likely to alter the geographic ranges of pests and diseases and the pressure they exert on potato production (Haverkort and Verhagen (2008)). As a consequence, breeders may need to alter some of their priorities.

6.4 TPS

As mentioned earlier, in the torrid zones of the lowland tropics and subtropics, cultivars based on current methods of true potato seed (TPS) propagation are an attractive proposition. The aim is still high yield and acceptable uniformity. If they could be produced, apomictic potatoes would be a solution to the uniformity problem. Furthermore, synthetic seed is an alternative to TPS that would avoid the need to develop parents that generate uniform hybrids. Hence there is currently renewed interest in somatic embryogenesis in potato, and sufficient progress has been made for serious consideration to be given to exploiting synthetic potato seed, as seen in the review by Veilleux (2005).

6.5 Breeding Objectives and Selection Criteria

Breeding objectives will vary from country to country, but all programs are likely to involve selection for higher yield, appropriate maturity and dormancy, tuber characteristics that affect quality and suitability for particular end uses, and resistance to abiotic and biotic stresses. To be of practical benefit, however, objectives need to be translated into the improvements required over existing cultivars and into selection criteria that can be used by breeders. The objectives and criteria that follow are all relevant to current breeding goals, but priorities will need to be assigned in any particular program as progress is most noticeable where the focus is on few rather than many traits. More details on each trait and its inheritance can be found in the review by Bradshaw (2007b). Not included are physiological and morphological parameters of crop growth, root architecture, and water and fertilizer use efficiency, but these could well become integrated into future breeding programs.

6.5.1 Yield, Dry Matter Content, Maturity, and Dormancy

High fresh-weight yield
Stability of yield across target environments and years
Tuber number and size appropriate for end use
Dry matter (specific gravity) and starch content appropriate for end use
Maturity appropriate for growing season
Dormancy appropriate for length of storage

6.5.2 Tuber Shape and Defects

Regular shape and shallow eyes to reduce wastage
Round shape for crisps (chips) and long oval for French fries
Lack of external defects (growth cracks, mechanical damage and bruising, and greening)
Lack of internal defects (hollow heart, brown center, and internal rust spot)

6.5.3 Nutritional and Health Value, Pigmentation, and Glycoalkaloids

Higher contents of antioxidant pigments: carotenoids (yellow flesh) and anthocyanins (red and purple flesh)
Increased vitamin C content
Increased micronutrient content (biofortification)
Glycoalkaloid content below 20 mg/100 g fresh weight
Reduced potential for acrylamide production in roasted and fried products (lower reducing sugars and asparagine)

6.5.4 Cooking and Processing Quality

Improved flavor (aroma and taste, volatile and non-volatile compounds)
Appropriate texture (ranges from waxy to floury (or mealy), dry matter and starch content, and even distribution for processing)
Freedom from after-cooking blackening and enzymic browning
Light-colored fry products post-harvest and after storage (lower reducing sugars)
Novel starches for countries with a starch industry (altered ratio of amylopectin to amylose)

6.5.5 Resistance to Abiotic Stresses

Resistance to water stress (drought avoidance, drought tolerance, and water-use efficiency)
Heat tolerance
Cold tolerance
Salinity tolerance
Mineral deficiency tolerance

6.5.6 Resistance to Major Pests

Potato tuber moth (PTM, *Phthorimaea operculella* Zeller): larvae mine foliage, stems and tubers in field and storage, most serious insect pest worldwide, particularly in warm tropical and sub-tropical climates.
Colorado potato beetle (CPB, *Leptinotarsa decemlineata* Say): can defoliate crop in field, major pest in northern latitudes, particularly in North America, Europe, Russia, and Central Asia.
Andean potato weevil (APW, *Premnotrypes* spp.), green peach aphid (GPA, *Myzus persicae*, primarily as virus vector), and leafminor flies (LMF, *Liriomyza huidobrensis*): major pests in many developing countries.
Cyst nematodes (*G. rostochiensis* Woll. and *G. pallida* Stone): penetrate and feed on roots, most damaging nematodes worldwide.
Root-knot nematodes (*Meloidogyne* spp.): the southern root-knot nematode (SRN, *M. incognita*) is the main problem in warm climates, whereas the Columbia root-knot nematode (CRN, *M. chitwoodi*) and the northern root-knot nematode (NRN, *M. hapla*) are the main ones in temperate regions, with *M. chitwoodi* and *M. fallax* emerging problems in Europe.

6.5.7 Resistance to Major Diseases

Oomycete Disease of Foliage, Stem, and Tubers

Late blight (*P. infestans* (Mont.) de Bary): the most serious disease of potato worldwide.

Fungal Diseases of Foliage, Stem, and Tubers in Warm Climates

Verticillium wilt (*Verticillium dahliae* Kelb.): most common soil-borne disease
Early blight (*Alternaria solani* (Ellis and Martin) Jones and Grout): most common air-borne disease
Fusarium wilt (*Fusarium solani* (Mart) App. and Wr. var. *eumartii* (Carp.) Wr. and *F. oxysporum* Schlecht.): soil-borne disease

Fungal Diseases of Tubers

Wart (*Synchytrium endobioticum* (Schilb.) Perc): persistent soil-borne, disfiguring, blemish-forming disease of tubers
Powdery scab (*Spongospora subterranea* (Wallr.) Lagerh): persistent soil-borne, disfiguring, blemish-forming disease of tubers
Dry rot (*Fusarium coeruleum* (Lib.) ex Sacc.), *F. sulphureum* (Schlecht.), *F. sambucinum* (Fuckel), and *F. avenaceum* Sacc. (Corda ex. Fr.): tuber-borne disease, important cause of spoilage of tubers in storage in warmer climates
Gangrene (*Phoma foveata* Foister): tuber-borne disease, was important cause of spoilage of tubers in storage in northern Europe
Black scurf (*Rhizoctonia solani* (Kühn.) and stem canker): tuber-borne blemish disease
Skinspot (*Polyscytalum pustulans* (Owen and Wakef.) M.B. Ellis): tuber-borne blemish disease
Silver scurf (*Helminthosporium solani* Dur. and Mont.): tuber-borne blemish disease
Black dot (*Colletotrichum coccodes* (Wallr.) Hughes): tuber-borne blemish disease

Actinomycete Disease of Tubers

Common scab (*Streptomyces scabies* (Thaxt.) Waksman and Henrici): persistent soil-borne, disfiguring, blemish-forming disease of tubers

Bacterial Diseases of Foliage, Stem, and Tubers

Bacterial wilt or brown rot (*Ralstonia solanacearum* Smith): the most serious disease of potato after late blight in the developing world.
Blackleg (stem) and soft rot (tuber in storage) (*Pectobacterium* spp.): *P. carotovorum* subsp. *atrosepticum* is common in temperate climates whereas *P. chrysanthemi* predominates in warmer areas and *P. carotovorum* subsp. *carotovorum* is well adapted to both climatic regions.
Bacterial ring rot (*Clavibater michiganensis* subsp. *sepedonicus* (Spieck and Kotth.) Davis et al.): a recurring seed-tuber-transmitted disease problem in temperate regions, despite many countries treating it as a quarantine disease and having a zero-tolerance policy for the import of seed potatoes.

Viral Diseases

PLRV (*Potato leafroll virus*): the most damaging and widespread of the viruses, aphid transmitted in a persistent manner
PVY (*Potato virus Y*): next in importance, aphid transmitted in a nonpersistent manner and hence harder to control with aphicides
PVA (*Potato virus A*): worldwide distribution
PVX (*Potato virus X*): worldwide distribution
PVM (*Potato virus M*): can be a devastating virus in the seed and ware potato production areas of Central and Eastern Europe
PVS (*Potato virus S*): worldwide distribution
TRV (*Tobacco rattle virus*): locally important in cooler climates, transmitted by Trichodorid nematodes, causes spraing symptoms in tubers, a particular problem for processors
PMTV (*Potato mop-top virus*): locally important in light sandy soils, transmitted by *Spongospora subterranea*, causes spraing symptoms in tubers, a particular problem for processors
PSTVd (*Potato tuber-spindle viroid*): a true seed-transmitted disease which is treated as a quarantine disease in countries where it is not endemic

7 Breeding Methods and Techniques

7.1 Breeding Cultivars at the Tetraploid Level for Clonal Propagation

7.1.1 Parents and Crossing

Potato breeding worldwide has traditionally involved making crosses between pairs of parents with complementary phenotypic features and this is still the main route to new cultivars. Increasingly parents will have genes introgressed from wild species and they may also be from complementary groups of germplasm to exploit yield heterosis (Bradshaw, 2009b). The aim is to generate genetic variation on which to practice phenotypic selection across a number of vegetative generations for clones with as many desirable characteristics as possible for release as new cultivars. As genetic knowledge of the potato accumulates, it will become easier to choose parents known to possess desired major genes and large-effect QTLs and to select genotypically for these in their offspring. Major genes have already been mapped for flesh, skin, and flower color, for tuber shape and eye depth, and for resistances to late blight, cyst nematodes, root-knot nematodes, viruses (PVY, PVA, PVX, PVM, PVS, and PLRV), and wart (Bradshaw, 2007b; Jansky, 2009). Large-effect QTLs have also been mapped for total glycoalkaloid content (TGA), maturity and resistances to late blight, Verticillium wilt, cyst nematodes, and PLRV (Bradshaw, 2007b; Bae et al., 2008; Sorensen et al., 2008; Finkers-Tomczak et al., 2009). In contrast, many economically important traits are still best viewed as complex polygenic traits,

despite a number of QTLs being found, and these include dormancy, dry matter and starch content, fry color, resistance to *Pectobacterium* (*Erwinia*), tuberization, and yield. For these traits breeders will still have to rely primarily on phenotypic data and the concepts of quantitative genetics to determine crossing strategy. With a highly heritable trait like fry color the midparent value is a good predictor of the mean performance of the offspring and a few carefully chosen crosses can be made (Bradshaw et al., 2000a). In contrast, with only a moderately heritable trait, such as yield, offspring mean is less predictable and more crosses need to be made to ensure that they include the best possible ones.

Today most cultivars come from deliberate artificial hybridizations. The floral characteristics of potatoes and methods of artificial hybridization and self-pollination have been described by Plaisted (1980). Details can also be found in Caligari (1992), Douches and Jastrzebski (1993), and in the textbook on *Breeding Field Crops* by Sleper and Poehlman (2006). A temperature of 19°C and 16 h of daylength are recommended for crosses involving *S. tuberosum* group Tuberosum so that an extension of natural daylength is required for crossing in the tropics and subtropics. In contrast, group Andigena is in effect day-neutral for flowering, but not of course for tuberization. Not all desired crosses are successful as problems can arise from clones failing to flower, buds and flowers dropping either before or after fertilization, low pollen production, and failure to produce viable pollen (male sterility). Breeders usually encourage flowering by the periodic removal of daughter tubers and sometimes graft young potato shoots onto tomato or other compatible *Solanaceous* plants. Stems with flowers attached can also be cut and placed in jars of water with an anti-bacterial agent to reduce contamination (Peloquin and Hougas, 1959).

7.1.2 Clonal Generations

Potato breeding at SCRI before 1982 was typical of most relatively large programs, both then and now (Mackay, 2005; Bradshaw, 2007a, 2009a). The seeding generation (SG) in the glasshouse comprised 100,000 genetically unique seedlings from some 200–300 crosses. Visual selection reduced this number of potential cultivars to 1,000 clones in replicated yield trials at a ware site in the third clonal generation (TCG). The first clonal generation (FCG) comprised 50,000 spaced plants at a high-grade seed site with a short growing season, rather atypical of normal ware production. The second clonal generation (SCG) of 4,000 unreplicated three- or four-plant plots was also grown at the seed site. Decreasing numbers (1,000, 500, and 200) of potential cultivars were then assessed for 3 years in replicated yield trials at a local ware site before the most promising ones (60, 10, and 5) underwent 3 years of more extensive testing at a number of sites, including overseas ones. One or a few clones would then be entered into 2 years of official statutory trials (National List Trials) and registered for Plant Breeders' Rights. Multiplication from disease-free stock would start with a view to commercialization. During these intermediate and final stages of selection the production of seed tubers was separated from the trials that were grown under ware conditions, designed as far as possible to resemble

Fig. 1.4 Early generations (spaced plants and unreplicated small plots) of potato breeding program at seed site in Scotland (*top*) and replicated yield trials at ware site in Scotland (*bottom*) (Source: SCRI)

those of good commercial practice (Fig. 1.4). Clones undergoing selection were assessed for their yield and agronomic performance, external and internal defects, and cooking and processing characteristics, as described by Bradshaw et al. (1998, 2003). They were also assessed for their disease and pest resistance in special tests as described by Mackay (1987) and Bradshaw et al. (2000b). More recently the time from seedlings to cultivar has been reduced by 3 years by using progeny tests to discard whole progenies, by starting replicated trials earlier at more than one site and by using micropropagation to multiply promising clones for more extensive testing (Mackay, 2005). More detailed information on handling the intermediate and later generations, including the conduct of yield trials and selection for disease and pest resistance, can be found in the review by Bradshaw (2007b).

Research in the 1980s found that intense early-generation visual selection for most quantitative traits was very ineffective, particularly between seedlings in a glasshouse and spaced plants at a seed site (Bradshaw and Mackay, 1994; Bradshaw et al., 1998). Selection for tuber skin and flesh color and shape can, however, be done if these are important for particular consumers. The solution to ineffective

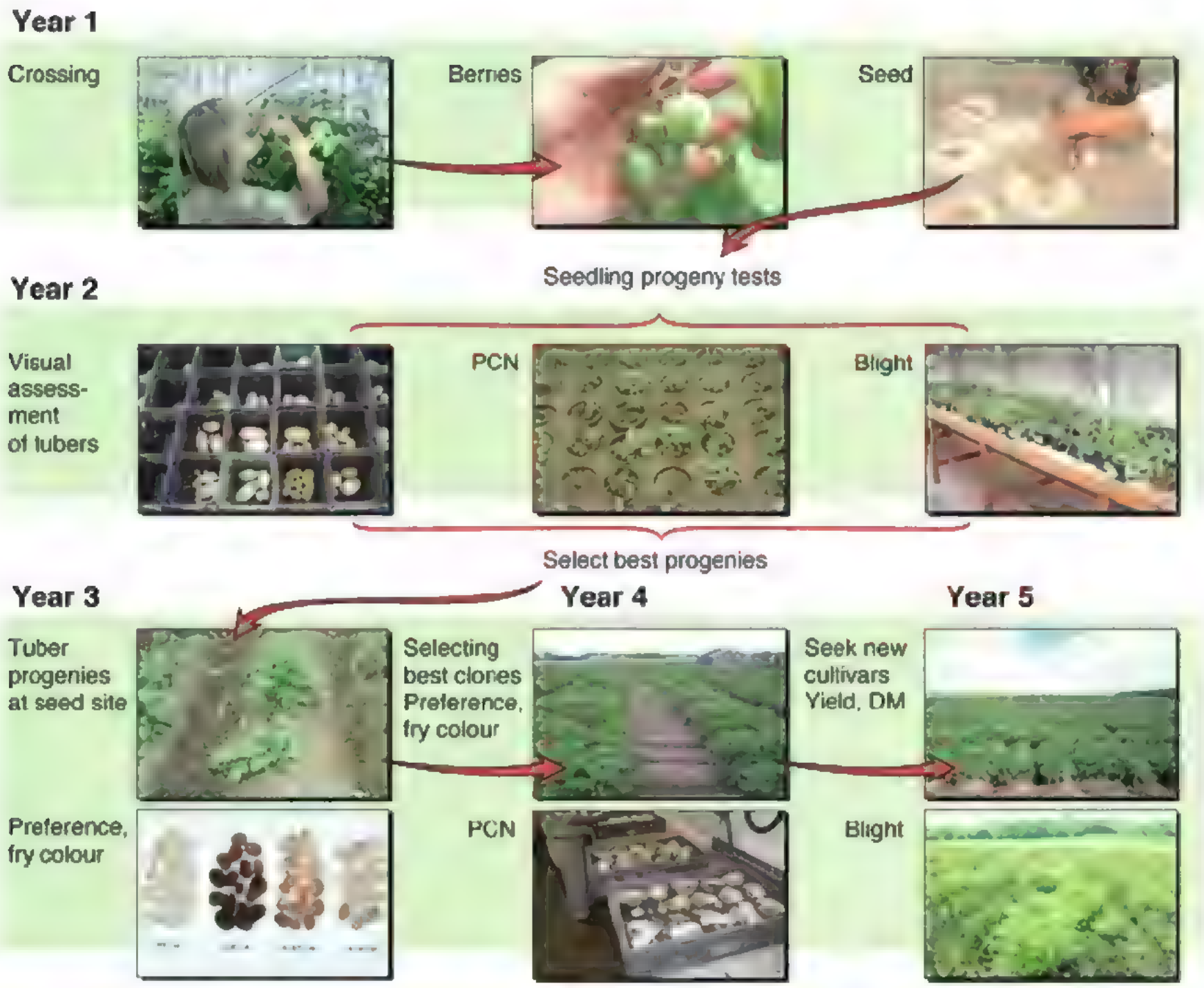

Fig. 1.5 Potato breeding at SCRI: progeny tests used to discard whole progenies (= full-sib families) in years 2 and 3, followed by clonal selection within best families in year 4 (unreplicated small plots at seed site) and in year 5 (yield trials at ware site), followed by further clonal selection and next round of crossing and selecting (Source: SCRI)

early-generation visual selection developed and implemented at SCRI was the use of progeny tests to discard whole progenies (= full-sib families) before starting conventional within-progeny selection at the unreplicated small-plot stage (Bradshaw and Mackay, 1994; Bradshaw, 2007a, 2009a). Today at SCRI, once promising clones have been identified after both the first and the second year of ware (yield) trials, they are used as parents in the next round of crossing and selecting to keep the momentum of the program going (Fig. 1.5).

7.2 Introgression

Introgression of genes from wild and cultivated species was introduced in Section 5.3. Introgression is essentially backcrossing, and in the past it took from three to seven backcrosses to transfer a major dominant resistance gene into a successful cultivar (Ross, 1986). Molecular marker-assisted introgression offers the possibility of faster progress than can be achieved by traditional backcrossing (Hermsen,

1994; Barone, 2004; Iovene et al., 2004). This is because one can select genotypically against the unadapted species genome as well as genotypically for the desired gene(s). With adequate molecular marker coverage of all 12 potato chromosomes, it is possible to estimate the optimal combination of population sizes and number of backcross generations and to select in a very precise way for the desired products of meiosis in each backcross generation (Hospital, 2003). But one is still dependent on the occurrence of favorable intra-chromosomal recombination and linkage drag (retaining undesirable genes through linkage to selected gene(s)) can be a problem. The recurrent parent(s) will be from tetraploid group Tuberosum when the starting material is one of the following: somatic hybrids between tetraploid *S. tuberosum* and primitive diploid (1EBN) species such as *S. bulbocastanum*; autotetraploids produced by colchicine treatment of diploid (2EBN) species such as *S. vernei*; and hexaploid (4EBN) species such as *S. demissum.* In contrast, the recurrent parent(s) will be from diploid (dihaploid) group Tuberosum, diploid group Phureja, or diploid group Stenotomum when introgression is from a 2EBN wild species. A comparison of tetraploid and diploid introgression was made by Bradshaw and Ramsay (2005).

Where introgression is performed at the tetraploid level, the result may not be a genotype with 48 Tuberosum chromosomes, including one (or more) of which has the introgressed gene(s). This need not affect the performance of the genotype and its vegetative propagation but could affect its fertility and use as a parent for further breeding. The result of an introgression from *S. brevidens* was a high-yielding clone, C75–5+297, with resistances to both tuber soft rot and early blight (Tek et al., 2004). Molecular and cytogenetic analyses revealed that C75–5+297 had 47 chromosomes, including four copies of chromosome 8, three from potato and one from *S. brevidens* that was the only part of the wild species genome present. In contrast Barone et al. (2001) did obtain 48 chromosomes and evidence of recombination between *S. commersonii* (a 1EBN diploid) and *S. tuberosum* chromosomes in their molecular marker-assisted introgression of tuber soft-rot resistance.

As potatoes are heterozygous outbreeders, use of the same recurrent parent during introgression results in a self of the recurrent parent and hence inbreeding depression. This can be avoided by using different Tuberosum parents for each backcross, but results in an entirely new cultivar, which may or may not be the desired outcome. The only way to introduce a gene into a known cultivar is by genetic transformation, which is discussed in a later section. It also has the advantage of no linkage drag and hence should be cleaner and faster.

7.3 Base Broadening and Population Improvement

Broadening the genetic base of modern breeding programs was considered in Section 5.5. All of the schemes considered were in essence population improvement for a number of generations (recurrent selection) to provide tetraploid or diploid parents suitable for crossing with adapted tetraploid parents (often cultivars) in the breeding of finished cultivars. Some of the schemes involved selection for

tuberization in long days. These were usually simple phenotypic mass selection schemes, but sometimes involved within family selection (Haynes and Lu, 2005). The rate of progress depends to a large extent on the length of each cycle. The Neotuberosum program of Simmonds (1969) operated on a 2-year cycle. In the first year large populations of seedlings were grown in the field and selected for high yields of tubers of acceptable sizes, shapes, and colors. In the second year the selected tubers were planted in an isolation site and open-pollinated berries harvested to provide the next generation of seedlings. In the USA Plaisted (1987) introduced the deliberate pollination of selected clones with bulk pollen to avoid inbreeding depression from selfing in his Neotuberosum program. He also achieved more vigorous plants for selection by raising his seedlings in pots to produce seed tubers for planting field trials. This enabled him to screen the seedlings in the glasshouse for resistance to late blight and viruses, but it also increased the length of each cycle to 3 years.

The diploid breeding program of Carroll (1982) relied on natural insect pollination and seed set and included both seedling and tuber populations with a minimum generation cycle of 2 years. In practice the generation time was 3 years once seedlings were raised in a polythene tunnel rather than the field. The self-incompatibility of the diploids was presumed to ensure cross-pollination. The diploid program of Haynes (Haynes and Lu, 2005) involved selection within 72 half-sib families and operated on a 2-year cycle for 10 generations, the first five to six for general adaptation followed by four to five for high specific gravity. The program was then continued on a 4-year cycle in which a seedling generation in the glasshouse was followed by 3 years of field evaluation in which the number of clones per family was reduced from 100 through 4 to 1. Open-pollinated seed was collected from the 288 clones evaluated in the second year in the field, but only used from the 72 clones selected after the third year in the field.

At SCRI, Bradshaw et al. (2009) have shown that full-sib family selection in a tetraploid breeding program can operate on a 3-year cycle with limited within family selection and on a 5- or 6-year cycle with more extensive within family selection. They recommended the 5- or 6-year cycle once genes have been combined from sufficient parents to achieve the program's objectives, in their case combining resistances to late blight and cyst nematodes with increased yield and acceptable fry color.

7.4 Breeding Cultivars for True Potato Seed

Breeding cultivars for TPS was started at CIP in 1972 with the aim of high yields and acceptable uniformity. None of the current breeding methods can deliver genetic uniformity and hence all of them involve selection for acceptable uniformity. Current TPS breeding aims to produce tetraploid cultivars, either from $4x \times 4x$ crosses in which heterosis is exploited between group Tuberosum and group Andigena (Simmonds, 1997) or from $4x \times 2x$ crosses in which the $2x$ parent produces a high frequency of $2n$ gametes by FDR so that 83% of its heterozygosity is

transmitted to the offspring (Golmirzaie et al., 1994; Clulow et al., 1995) or from $2x \times 2x$ crosses in which both parents produce $2n$ gametes, again with a very high frequency of $2n$ pollen produced by FDR (otherwise the offspring will contain more diploids than tetraploids) (Ortiz and Peloquin, 1991). Simmonds (1997) argued, however, that diploid TPS cultivars should not be ruled out for the future, and De Maine (1996) produced TPS families of long-day-adapted Phureja that appeared as uniform for tuber size and shape as selected clones. Open pollination of diploids will result in almost 100% outcrossing because of self-incompatibility. Cross-pollination between field plots of *S. phureja* has been estimated to decline from 5.1% at 10 m to 0.2% at 80 m (Schittenhelm and Hoekstra, 1995), figures which can be used to decide isolation distances for natural true-seed multiplication. Open pollination of tetraploids will normally result in varying amounts of self-pollination and inbreeding depression, which may not be outweighed by their apparent intrinsic yield advantage over diploids. Furthermore the seed fertility (seed yield) of diploids is greater than that of tetraploids. Whether or not diploid inbred lines and true F1 hybrids can be produced in the future for maximum heterosis and uniformity is a matter for further research. The inbreeding depression from selfing meant that hand-pollinated tetraploids were superior to open-pollinated ones, but their production was more expensive because of the cost of emasculation of the flowers of the female parent (Simmonds, 1997).

Today, the technology to produce hybrid TPS uses male sterility to minimize hybridization costs and mother plant management to increase seed production (Chujoy and Cabello, 2009). One hundred to 150 kg TPS can be produced from 1 ha. In large TPS seed stocks, dormancy is released by high temperature treatment for 4–6 months. TPS is sown in seedbeds to produce minitubers or to raise seedlings for transplanting to the field. The seedling transplants, or more successfully the minitubers, are then used to produce either seed tubers or potatoes for consumption. The seed tubers derived from TPS cultivars should ideally be selected for tuber traits each generation to ensure that the produce is within the desired yield and quality range.

7.5 Genetically Modified Potatoes

Genetic modification is the act of inserting one or more agriculturally important genes into the genome of a potato plant by in vitro techniques and by using modified *A. tumefaciens* as a natural gene transfer tool (Jacobsen, 2007). It thus allows targeted improvements of successful and widely grown potato cultivars. Today marker-free transformants can be produced, most easily by using transformation vectors without selection markers. PCR analysis of regenerated plants has shown relatively high percentages (5%) of transformation (Jacobsen, 2007). The products of transformation do require screening to select the best transformants for commercialization, including demonstration of substantial equivalence to the parent cultivar (Davies, 2002). Commercialization also involves the demonstration that it is safe both to grow and eat the genetically modified (GM) potatoes. While no GM potatoes are currently being grown commercially, prospects are good for the future provided skeptical consumers can be convinced of their value.

Today a distinction needs to be made between transgenic, intragenic, and cisgenic potatoes. Cisgenes are genes from cultivated potatoes and their cross-compatible wild relatives. A cisgene includes its native introns and is flanked by its native promoter and terminator in their normal sense orientation. These restrictions do not apply to intragenes. They are produced by isolating specific genetic elements from cultivated potatoes and their cross-compatible wild relatives, rearranging (recombining) them in vitro to create 'intragenic' DNA, and then inserting the resulting expression cassettes into a potato using plant-derived transfer DNAs (P-DNAs) and marker-free transformation. P-DNAs resemble *Agrobacterium* T-DNA borders that can be used to support DNA transfer from *Agrobacterium* to plant cells creating 'intragenic' plants (Rommens et al., 2007). Finally, transgenes are ones derived from other organisms (e.g., bacteria and fungi) or other plant species which are not cross-compatible with cultivated potatoes.

7.5.1 Genes from Cultivated Potatoes and Their Cross-Compatible Wild Relatives

Desirable (dominant) genes can be found in cultivated potatoes and their cross-compatible wild relatives, cloned, and introduced by genetic transformation. Gene isolation in potato can be done via map-based (i.e., position-based) cloning using BAC technology and dense AFLP genetic maps, but it is time consuming (De Jong, 2005). Sometimes shortcuts can be taken by using a candidate gene approach or allele-mining, but their success is not guaranteed. However, gene isolation should be much faster now that the potato genome has been sequenced (see Section 8.1). Past examples are the molecular cloning of natural resistance genes and their transfer into well-adapted but susceptible cultivars (see book chapter by Simko et al., 2007). Currently there is a major research effort in the Netherlands (DuRPh Program) using cisgenic modification of potatoes in a quest for durable resistance to late blight (Haverkort et al., 2009). In 2009, for the first time, they trialled potatoes in which they had stacked two resistance genes (R-genes) by marker-free cisgenesis.

7.5.2 Gene Silencing

Where the control of biochemical pathways of interest is understood, down-regulation of gene expression using gene silencing has proved useful for achieving some desired modifications, in particular to starch composition, processing traits, and other quality traits (see review by Bradshaw, 2007b). The gene silencing has been achieved by RNA interference in the broadest sense (i.e., post-transcriptional gene silencing) and mimics recessive loss of function mutations (Jacobsen, 2007). For example, in antisense technology the potato plant is induced to produce large amounts of antisense RNA capable of trapping the messenger RNA from the gene being transcribed in an untranslatable RNA duplex. However, of particular current interest are the intragenic potatoes which are being trialled from the Simplot Program in the USA in which three genes are silenced. They combine reduced black spot bruise (polyphenol oxidase (*Ppo*) gene) with lower reducing sugars out

of cold storage, reduced amounts of processing-induced acrylamide, and increased starch levels (starch degradation-associated *R1* and phosphorylase-L (*PhL*) genes) (Rommens et al., 2006). The Simplot Program has also been able to achieve low-acrylamide French fries and potato chips (crisps) by tuber-specific silencing of two asparagine synthase genes (Rommens et al., 2008). Glasshouse-grown tubers of the transformed intragenic plants contained up to 20-fold reduced levels of free asparagine and both their French fries and potato chips accumulated as little as 5% of the acrylamide present in the controls. Tuber yield, shape, and sensory characteristics were not affected.

7.5.3 Novel Traits

Finally, and more controversially, the use of exotic sources of genes in transformation has the clear value of permitting the introduction of traits not found in cross-compatible relatives and hence of novel function. The genes used to date have mainly been ones that code for proteins that are toxic to pests and pathogens, ones whose expression interferes with virus multiplication in host cells, and ones that code for key enzymes in biochemical pathways in other organisms, often, but not always other plant species. Examples can be found in the book chapter by Bradshaw (2007b), but typical ones can be briefly summarized as follows.

Resistance to the Colorado potato beetle (Duncan et al., 2002) and the potato tuber moth (Mohammed et al., 2000; Davidson et al., 2004; Douche and Grafius, 2005) has been achieved with genes that encode proteins from the bacterium *B. thuringiensis*; to the potato cyst nematodes with genes that encode cysteine proteinase inhibitors (cystatins) (Urwin et al., 2003); to viruses PLRV and PVY with replicase and coat protein genes, respectively, from these viruses (Duncan et al., 2002); and to blackleg and soft rot with a gene encoding a chicken lysozyme enzyme (Serrano et al., 2000). Expression of a gene for a derivative of the antimicrobial peptide dermaseptin B1, from the arboreal frog *Phyllomedusa bicolor*, has been shown to increase resistance to diseases, such as late blight, dry rot, and pink rot, and to markedly extend the shelf life of tubers (Osusky et al., 2005). Protein content has been increased and amino acid balance improved by expression of a non-allergenic seed albumin gene (*AmA1*) from *A. hypochondriacus* (Chakraborty et al., 2000), and carbohydrate composition has been improved by inulin production from the expression of fructosyltransferases from globe artichoke (*C. scolymus*) (Hellwege et al., 2000). The primary flavor compound methional has been enhanced by increasing the level of soluble methionine (Di et al., 2003). Carotenoid content has been improved, including the production of beta-carotene from expressing an *Erwinia uredovora crtB* gene encoding phytoene synthase (Ducreux et al., 2005) and the production of astaxanthin from expressing an algal (*Haematococcus pluvialis*) *bkt1* gene encoding beta-carotene ketolase (Morris et al., 2006). The conversion of sucrose to glucose and fructose, and hence cold sweetening, has been minimized by expressing a putative vacuolar invertase inhibitor protein from tobacco (Greiner et al., 1999).

8 Integration of New Biotechnologies in Breeding Programs

We have just considered progress in the production of genetically modified potatoes. Earlier we saw how potato breeders can use somatic (protoplast) fusion to achieve difficult or impossible sexual hybridizations, androgenesis (anther culture) for haploidization, and embryo rescue to secure a hybrid where embryo abortion is due to a defective endosperm. We also saw that today somaclonal variation tends to be viewed as a source of undesirable variants that need to be screened out of breeding programs that involve plant regeneration and that the potato is not ideal for deliberate mutation breeding because it is a clonally propagated tetraploid crop (it is easier to achieve loss of function by gene silencing). In contrast, somatic embryogenesis holds promise as an alternative to TPS. In the next section we shall see how micropropagation has become a key aspect of the production of clean seed tubers for planting material. In this section we need to consider the impact of advances in genetics for gene discovery and marker-assisted selection.

8.1 Gene Discovery (Linkage Maps, Sequencing, and Microarrays)

During the last 20 years, at least a dozen linkage maps have been constructed with DNA-based markers, mostly in experimental populations of diploid potato (Celebi-Toprak et al., 2005; Gebhardt, 2007a, b). Many qualitative and quantitative traits have been mapped onto potato chromosomes. Knowing their map positions was instrumental for cloning the major genes mentioned earlier, identifying candidate genes underlying quantitative traits, and developing diagnostic markers for use in marker-assisted selection, which is considered in the next section. Diagnostic markers are also being developed through association mapping and population genetics in tetraploid varieties and breeding lines (Gebhardt, 2007a).

The first draft DNA sequence of the potato genome (840 Mb) was published on September 23, 2009 (http://www.potatogenome.net). In fact two potato 'varieties' were sequenced, RH, a diploid, heterozygous potato variety and DM, a doubled monoploid. The initial choice of the Dutch-led sequencing consortium was RH. A potato genomic bacterial artificial chromosome (BAC) library of 78,000 clones was fingerprinted and aligned into about 7,000 physical map contigs. The BAC ends were sequenced and approximately 30,000 BACs were anchored to the ultra-high density genetic map of potato, composed of 10,000 unique AFLP^{TM} markers. A BAC by BAC sequencing strategy was then adopted but overall progress was slow. The heterozygosity of RH limited the progress of physical mapping and was expected to complicate assembly of genome sequence. Hence whole genome shotgun sequencing of DM was undertaken as it was expected to eliminate the complexity in assembly. The consortium is now working on high-quality drafts of both genomes, the results of which should aid gene discovery and the development of molecular breeding methods.

Progress is also being made in understanding gene expression and how gene function at the biochemical level relates to observed phenotypes. Where genetic

and biochemical information is available on metabolic pathways, such as those for carbohydrates, anthocyanins, and carotenoids in potatoes, candidate genes are being postulated and sought for improving both qualitative and quantitative traits. For example, Zhang et al. (2009) have confirmed that the potato *R* locus codes for dihydroflavonol 4-reductase and that a specific allele of the *dfr* gene is required for the production of red pelargonidin-based anthocyanin pigments. Furthermore, advances in metabolite profiling are allowing a systems approach to understanding biochemical pathways and hence the key genes to target for desired phenotypic (trait) changes. By 2006 there were about 220,000 EST (expressed sequence tags) sequences for potatoes in the public database GenBank (http://www.ncbi.nlm.nih.gov) and these can be regarded as a catalogue of partially sequenced genes that are expressed in target potato cells and organs of interest for crop improvement. The value of ESTs for gene discovery, identifying candidate genes and developing markers, will increase as they are located on the genetic and physical maps of potato, and as the extent of colinearity of the different Solanaceae genomes is established. Colinearity can be exploited in comparative genomics where known gene position and function in one genome are used to make inferences to other genomes (e.g., from tomato to potato, pepper, and eggplant). The availability of considerable quantities of EST data facilitated the development of microarrays for global gene expression studies in which different genotypes (e.g., cultivars and breeding clones) can be compared in different environmental situations, including the presence of pests and diseases. The Potato Oligo Chip Initiative (POCI) of Wageningen University in the Netherlands uses the Agilent '44 K feature platform' system. Their microarrays contain at least 75% of the potato transcriptome (messenger RNAs = expressed genes) and they should allow a more complete analysis of gene expression than has previously been possible.

8.2 Marker-Assisted Selection

As knowledge increases about the number and chromosomal locations of genes affecting important traits, breeders should be able to design better breeding programs. The advantages of molecular marker-assisted introgression were considered in the previous section. We now need to consider a tetraploid program where breeders will be able to choose parents that complement one another for desirable genes and then select for these genes in the offspring. Breeders will be able to determine the seedling population size required for certainty of finding the desired combination of genes or, more realistically, the number of cycles of crossing and selection required before this is achievable in practice in the size of population that they can handle. A big impact on the efficiency and rate of progress would be the identification of superior clones with the desired combination of genes as seedlings in the glasshouse and the use of modern methods of rapid multiplication to progress them to commercialization. This will require molecular marker-assisted selection (MAS) or preferably direct recognition of the desired genes, as has recently been

achieved for the *RB* gene for late blight resistance from *S. bulbocastanum* (Colton et al., 2006). Progress to date has been slow but is expected to increase.

Diagnostic markers are ones that have a very high probability of detecting the desired gene and hence are of value to breeders. Examples of ones for major genes for disease resistance are as follows. Kasai et al. (2000) developed sequence characterized amplified region (SCAR) markers to the *Ry* gene (from group Andigena, on chromosome 11) for extreme resistance to PVY. Bakker et al. (2004) identified an AFLP marker (EM1) that co-segregates with the *H1* gene for resistance to *G. rostochiensis* pathotype Ro1 and recommended its conversion to a cleaved amplified polymorphic sequence (CAPS) marker for use in marker-assisted selection because such markers are cheaper and easier to handle. Colton et al. (2006) developed a polymerase chain reaction (PCR)-based DNA marker for tracking the *RB* gene for resistance to late blight. Likewise, Sliwka et al. (2006) developed a PCR-based DNA marker for the *Rpi-phu1* gene (from group Phureja) for resistance to late blight. Finally, Gebhardt et al. (2006) demonstrated the use of diagnostic markers for *Rx1* (extreme resistance to PVX), *Sen1* (resistance to *S. endobioticum* pathotype 1, the cause of potato wart), and *Gro1* (resistance to all known pathotypes of *G. rostochiensis*), as well as *Ry*, for pyramiding these major genes for pathogen resistance in potato. The pyramiding of such major genes, together with QTL alleles of large effect for disease resistance, is likely to be the first main use of marker-assisted selection because of the removal of the need for costly, complex, and sometimes inaccurate disease testing. One of the sub-projects in the current EU Framework 6 Integrated Project BIOEXPLOIT is developing marker-assisted breeding for disease resistance in potatoes. Two examples of such MAS are the APPACALE program in Burgos, Spain and the Zamarte Breeding Company program in Kamien Kraj, Poland (Carrasco et al., 2009). Furthermore, the breeding programs at the Crops Research Centre, Oak Park, Ireland and the SCRI, Dundee, Scotland plan to use a diagnostic marker for a QTL of large effect ($GpaIV^{s}_{adg}$) for resistance to *G. pallida* Pa2/3 (Moloney et al., 2010).

9 Seed Tuber Production

TPS seed production was dealt with in Section 7.4. Here we are going to consider asexual reproduction which allows a genetically unique seedling to be maintained, multiplied, and grown as a new cultivar. A useful account of the various multiplication procedures can be found in a special issue of Potato Research, The Canon of Potato Science (Struik et al., 2007). Potato yields and quality are certainly best when crops are planted with disease-free seed tubers in the correct physiological state. Experience around the world during the twentieth century showed that this is most likely to be achieved through statutory seed certification schemes operating in areas where potatoes are grown only for seed. Such areas will usually be geographically and climatically less favorable to the aphid vectors of viruses which cause systemic infection (Jeffries et al., 2006). A typical seed production scheme with certification is now described.

Seed production starts from pathogen-free microplants which are produced by the certifying authority (or under license) in sterile laboratory conditions. In Scotland, for example, SASA (http://www.sasa.gov.uk) is the certifying authority for the Seed Potato Classification Scheme (SPCS). Single-node cuttings from tuber sprouts, from tubers supplied by the breeder, can be taken to provide rooted plantlets for pathogen testing. The breeder's stock should have been grown to a high health status and officially inspected and approved. If pathogen (mainly virus) elimination is required, larger plants can be grown from the plantlets and exposed to a heat treatment or to chemotherapy (e.g., Virozole) prior to meristem-tip culture. Dissected portions of the meristematic region of a shoot tip are placed on a liquid nutrient medium for plant regeneration. Once the resulting, or original, plantlets have been confirmed to be pathogen free, they can be used for rapid multiplication by in vitro nodal cuttings under artificial, aseptic conditions in the laboratory. The healthy plant material is cut into individual stem portions, each with one axial bud and an attached leaf (single-node cutting), which are placed on agar media in jars. The axial bud grows into stems with numerous buds from which more single-node cuttings can be taken. Once sufficient have been produced, they are allowed (with the help of growth regulators) to develop into fully rooted in vitro plantlets (transplants). These are then used by licensed commercial growers to produce minitubers (pre-basic TC (tissue culture)) in a greenhouse or screenhouse with high health status. The transplants can be grown in soil where they are likely to produce from two to five minitubers per plant. However, many more (up to 40) uniform tubers can be achieved from frequent harvests when the transplants are grown in aeroponic, hydroponic, or nutrient film cultures. In aeroponic culture the 'below-ground' plant parts are suspended in air and intermittently misted with nutrient solution. In hydroponic culture the transplants are grown in static nutrient solution whereas the nutrient flows along the lower roots in nutrient film culture. The minitubers are then grown by officially approved commercial growers in the field to produce pre-basic (field grown) seed tubers for further field multiplication. Subsequent generations result in grades of basic seed and finally certified seed in the amount required by ware growers who produce potatoes for consumption. Most European countries plant whole seed tubers whereas cut tuber pieces are commonly used in African, American, and Asian countries. There are usually from four to six field generations.

In Scotland seed crops are officially inspected twice during the growing season and tubers must also be inspected for diseases and disorders and meet the required standards before they can receive the official label required for marketing. The land used for seed crops must be free from wart disease and also tested and confirmed free from cyst nematodes. The interval between potato crops in the rotation must be 7 years for pre-basic seed crops and 5 years for basic seed crops. Certified seed can only be sold for ware, it cannot be replanted in Scotland. It is common practice for the certifying authority to hold in vitro pathogen-free nuclear stocks of cultivars under multiplication and also to fingerprint cultivars with molecular markers for unique identification (http://www.sasa.gov.uk).

Two other types of asexual reproduction are worthy of mention. First, it is easy to take and root stem cuttings from potato plants and this can be a useful way to

rapidly multiply potential cultivars for more extensive trialling in a breeding program. Second, in vitro plantlets can be induced to produce microtubers in the axils of leaves of cuttings. These can be of value for germplasm conservation and for storage and exchange of germplasm, but perhaps are of most value in potato research.

Finally it is important to point out that strict quarantine procedures are required when potatoes are transferred from one country to another to prevent the introduction of diseases, particularly non-indigenous ones. Again advances with in vitro techniques are proving useful. Lang (2001) has described how CIP supplies its new cultivars to farmers in East Africa through a seed multiplication scheme that starts in Kenya with nodal cuttings being taken from virus-free sprouts. These are supplied in vitro from CIP headquarters in Lima, Peru to the Quarantine Station in Kenya.

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